Growth, Biomass, and Production of a Small Unexploited Plaice Stock in St. Margaret's Bay, Nova Scotia

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ABSTRACT

Bakken, E. 1987. Growth, biomass, and production of a small unexploited plaice stock in St. Margaret's Bay, Nova Scotia. Can. Tech. Rep. Fish. Aquat. Sci. 1555: vii + 51 p.

As part of a general study of the processes controlling the productivity of marine organisms in St. Margaret's Bay, Nova Scotia, the American plaice (Hippoglossoides platessoides) was selected for a study of parameters determining the production of this dominant demersal fish stock. Samples were collected with small-meshed otter trawls and covered the entire Bay throughout the year; 8,686 plaice were tagged. Analysis of vertebrae numbers, tagging, observations of size shifts, etc., indicates that the Bay supports a local stock. Growth was determined from otoliths. The growth pattern resembles that found in other sub-arctic areas and is characterized by large sex differences, slow growth rates, and high longevity. Males are about 33 cm at Age 13, and females 56 cm at Age 24. A comparison of growth rates determined from length-at-age and back-calculated lengths revealed no "Lee's phenomenon," and hence growth as computed from length-at-age data does not result in underestimation of the true production. The 50% maturity point falls at near Age 6 for males and Age 11 for females. The sex ratio varies greatly among the size groups due to differential mortality between sexes, and the number of reproducing males exceeds that of the females. As the plaice stock is unexploited, the observed mortality reflects deaths by natural causes only. Catch curves and tagging showed that mortality increases when plaice become mature. For females the estimated instantaneous rates of mortality were 0.10 from Ages 4 to 10 and 0.37 from Ages 11 to 22. A high proportion of the plaice was infected by a lymphocystis disease.

Relative densities of plaice were determined from catches in 11 depth zones and related to estimates from the tagging experiments. An increase in number with depth was observed, accompanied by a decrease in size. Attempts were made to convert the relative abundance figures to estimates of numbers of plaice per unit area. The efficiency and the area swept by the trawl were observed by SCUBA divers. Based on this, the highest density of catchable plaice was calculated to be 745 per hectare, and near 90% of the catchable stock was in depths between 20 and 40 fm. The estimates of abundance were converted to biomass by the weight-length relationship $W=0.005489\ L^{3.099}$, and appropriate length distribution of each depth zone. The overall mean biomass of catchable plaice was 39.9 kg per hectare. The number of young plaice not fully vulnerable to the net was estimated, and the total biomass of the entire stock was found to be about 670 t in 138 km^2, equivalent to near 50 kg per hectare.

Production was calculated as total annual growth of the stock, based on increase in mean individual weight and number present between successive ages. The seabed area below 55 m, which accounts for 20% of the Bay, bears

near 70% of the estimated production; and the overall annual production of the catchable stock is about 7.6 kg per hectare. Production was also calculated from an Allen curve; and when plaice not fully vulnerable to the net are included, the figure becomes 10.0 kg per hectare. Roughly 1.2 kg is added by gonad production. Investigations of stomachs showed that young plaice feed heavily on crustaceans, larger plaice take more ophiuroids and polychaetes, while the largest also take large bivalves and sea urchins.

The relation between production and biomass is of particular interest, and the ratio P/B=0.21, the turnover rate, is discussed on the basis of predictions made from life length and average weight of the plaice. An attempt was made to estimate the food requirement of the stock and compare this with data on available food. It appears from this that the supply of food is not a limiting production factor.

RÉSUMÉ

Bakken, E. 1987. Growth, biomass, and production of a small unexploited plaice stock in St. Margaret's Bay, Nova Scotia. Can. Tech. Rep. Fish. Aquat. Sci. 1555: vii + 51 p.

Dans le cadre d'une étude générale des processus qui gouvernent la productivité des organisms marins dans la baie St. Margaret, Nouvelle-Écosse, on a choisi la plie canadienne (Hippoglossoides platessoides) pour étudier les paramètres qui déterminent la production de ce stock dominant de poissons démersaux. Les échantillons ont été prélevés par chalutage avec un filet à petites mailles et toute la baie a été échantillonnée au cours de l'année; 8 686 plies ont été marquées. L'analyse du nombre de vertèbres, le marquage, l'observation des changements de taille, etc., indiquent que la baie contient un stock local. La croissance a été déterminée à partir des otolithes. L'évolution de la croissance ressemble à celle que l'on observe dans d'autres zones sub-arctiques et est caractérisée par d'importantes différences liées aux sexe, par des taux de croissance lents et par une longévité élevée. Les mâles avaient une longueur d'environ 33 cm à l'âge 13 et les femelles, 56 cm à l'âge 24. Une comparison des taux de croissance déterminés à partir de la longueur par âge et de la retromesure a révélé qu'il n'y avait pas de "phénomène de Lee," et par conséquent, que la croissance calculée à partir des données de longueurs par âge n'entraînent pas une sous-estimation de la production réelle. Le point de maturité 50% se situe près de l'âge 6 dans le cas de mâles, et de l'âge 11 dans le cas de femelles. Le sex-ratio varie considérablement parmi les groupes de tailles à cause de la mortalité différentielle entre les sexes, et le nombre de mâles reproducteurs dépasse celui des femelles. Comme le stock de plies n'est pas exploité, la mortalité observée reflète les décès dus uniquement à des causes naturelles. Les courbes des prises et le marquage ont révélé que la mortalité augmente lorsque la plie atteint la maturité. Pour les femelles, les taux instantanés de mortalité estimés étaient de 0,10 de l'âge 4 à 10 et de 0,37 de l'âge 11 à 22. Une forte proportion des plies étaient atteintes de lymphocystite.

Les densités relatives des plies ont été déterminées à partir des prises effectuées dans 11 zones de profondeur et elles ont été reliées aux estimations obtenues à partir des expériences de marquage. On a observé une

augmentation du nombre de plies et une diminution de leur taille en fonction de la profondeur. Des tentatives ont été faites pour convertir les chiffres ayant trait à l'abondance relative pour obtenir des estimations du nombre de plies par surface unitaire. L'efficacité et la surface balayée par chalutage ont fait l'objet d'observations par des plongueurs sous-marins. A partir de ces observations, la densité la plus élevée de plies pêchables a été calculée comme étant de 745 par hectare, et près de 90% du stock pêchable se situait à des profondeurs variant de 20 à 40 brasses. Les estimations de l'abondance ont été converties en biomasse par la relation poids-longueur $W=0005489\ L^{3,099}$, et la distribution de longueurs propre à chaque zone de profondeur. La biomasse moyenne globale de plies pêchables était de 39,9 kg par hectare. Le nombre de jeunes plies qui n'étaient pas encore entièrement vulnérables au filet a été estimé et la biomasse totale du stock entier a été évaluée à environ 670 t dans une superficie de 138 km^2, l'équivalent de près de 50 kg par hectare.

La production a été calculée sous forme de croissance annuelle totale du stock, à partir de l'augmentation du poids individuel moyen et du nombre d'individus dans les âges successifs. La zone de fond marin située en dessous de 55 m, qui compte pour 20% de la baie, assure près de 70% de la production estimée et la production annuelle globale du stock pêchable est d'environ 7,6 kg par hectare. La production a également été calculée à partir d'une courbe d'Allen; lorsque les plies qui ne sont pas complètement vulnérables au filet sont incluses, le chiffre s'élève à 10,0 kg par hectare. La production gonadique ajoute à peu près 1,2 kg. L'étude du contenu stomacal révèle que les jeunes plies s'alimentent surtout de crustacés, que les plies plus grosses consomment plus d'ophiuridés et de polychètes, et que les plies le plus grosses se nourrissent également de gros bivalves et d'oursins.

La relation entre la production et la biomasse est d'un intérêt particulier, et le rapport P/B=0,21, le taux de renouvellement, est discuté en fonction des prévisions faites à partir de la longévité et du poids moyen de la plie. Une tentative a été faite pour estimer les besoins nutritionnels du stock et pour comparer les résultats obtenus avec les données sur l'alimentation accessible. Il ressort de cette étude que l'approvisionnement alimentaire n'est pas un facteur limitant de la production.

PREFACE

This study was conducted while the author was on a Post-Doctoral Fellowship with the former Marine Ecology Laboratory of the Bedford Institute of Oceanography during 1966, 1967, and 1968. The manuscript was completed following the Fellowship but never published. To facilitate broader distribution, it is issued as a Canadian Technical Report of Fisheries and Aquatic Sciences. The references are not up to date, but the observations and their analysis are still new and of considerable interest.

INTRODUCTION

Most studies of marine fish stocks deal with species exploited by a fishery. The major objective of these studies is to provide information needed to manage the fishery so that a maximum sustained yield, i.e. production to man, can be obtained. Very few investigations have been concerned with unexploited stocks of commercially important species, and data on biomass and production of such stocks are lacking. Data of this type are important to establish models of tropho-dynamics of fish ecosystems in order to study the mechanisms involved. A better knowledge of these mechanisms may form an improved basis for the management of the fisheries and ultimately increase yield.

The present study describes vital statistics of a discrete population of American plaice, Hippoglossoides platessoides (Fabricius) with calculations of biomass and production in relation to distribution and area. The data reflect the conditions of an unfished balanced fish stock.

The study is part of a general investigation of basic production processes and determinations of energy flow in St. Margaret's Bay. The estimate of the plaice production can be interpreted only when knowledge about the type, the available supply, and the efficiency of utilization of the food are determined. Studies of these problems, as well as measurements of production at other trophic levels, were undertaken by the Marine Ecology Laboratory (Bedford Institute of Oceanography, Dept. of Fisheries and Oceans, Dartmouth, N.S.).

MATERIALS AND METHODS

DESCRIPTION OF THE AREA

St. Margaret's Bay is located on the southern coast of Nova Scotia (Fig. 1). The Bay is about 18 km long and 5-10 km wide, narrowest at the mouth. The eastern shoreline is indented by shallow coves, and the western side is steep and rocky. The Bay is characterized by a sill at the mouth. The threshold depth is 51 m while the deepest part, in the southwestern portion, is 95 m. Extensive shallow areas are found in the Bay, and about half of the seabed is at depths less than 40 m.

The temperature at the bottom is generally low, and varies within a narrow range, except in shallow water. Typically, the bottom temperature in the summer is between 2.5°C and 3.5°C at all depths below 40 m and about 10°C at 10 m. In winter the surface temperature drops to near 0°C, and ice usually forms in the inner coves. The annual variation in the temperature at the bottom in the deeper parts, below 40 m, is very small. The lowest temperature, about 1.0°C, is found in early summer, with a gradual increase to 4.5°-5.5°C in early winter.

Bottom salinities show little variation throughout the year, with a range of 30.9-32.2°/∞ at 53 m (Platt and Irwin 1968).

The seabed below the 50 m depth is rather uniformly muddy. Typical sediment analysis shows 95% mud (particle diameter <0.06 mm) and 5% sand

(0.06-2.00 mm). In the area between 25 and 50 m the sediments are more variable, and generally coarser with mud content 10-75%, sand 15-80%, and gravel (>2.00 mm) 0-40%.

The demersal fish fauna can be classified as sub-arctic. Besides American plaice (Hippoglossoides platessoides), the most common fish species are: cod (Gadus morhua), winter flounder (Pseudopleuronectes americanus), haddock (Melanogrammus aeglefinus), thorny skate (Raja radiata), longhorn sculpin (Myxocephalus octodesemspinosus), witch flounder (Glyptocephalus cynoglossus), ocean pout (Macrozoarces americanus), snake blenny (Lumpenus lumpretaeformis), sea raven (Hemitripterus americanus), and monkfish (Lophius americanus).

The commercial fishery for groundfish in the Bay is almost negligible, and St. Margaret's Bay has been closed to trawling since 1953. Local fishermen set gillnets during the winter months, mainly to catch cod. Large plaice are caught in these nets, but have no market value.

SAMPLING METHODS

Samples of plaice were collected in 1966 and 1967, with a few additional samples in 1968. Most of the sampling was carried out during the summer months. Several vessels were used, but the main part of the sampling program was carried out with the "Whip-the-Wind," a chartered 45 ft stern dragger. Samples were also obtained with the research boat "Sigma-t," of similar design. The research vessels "Harengus" (84 ft) and "E.E. Prince" (135 ft) were used on a few occasions.

Sampling took place only during daylight hours.

All samples were collected with an otter trawl. On the two smaller vessels a standard flatfish trawlnet was used. The net measured 12.8 m along the footrope which was made from chain wound with hemp rope and not fitted with rollers. The mesh size was uniform throughout the net. Two sizes were used: "1½ inch" with measured average 3.6 cm stretch mesh, and "2½ inch" with average mesh 7.2 cm.

Standard ¾ No. 35 Yankee trawls were used on the two larger vessels. These nets had 10.1-12.7 cm mesh with 1.9 cm liner in the codend.

Experiments were conducted to calculate the mesh selection for the two flatfish trawls. Catches in a series of seven hauls with the small-meshed net and nine hauls with the large-meshed net were compared. From this a selection curve for the 2½ inch mesh net was established following the method of Beverton and Holt (1957, P. 222). The catches by the larger-meshed net exceeded those by the smaller beyond a fish length of 20 cm. Adjustments were required to obtain a true selection ogive, and the ratios of catches at each length were adjusted by extrapolating linear regression.

The selection curve obtained is given in Figure 2. The length at which 100% of the plaice is retained by the 2½ inch net is 23 cm according to this curve. This length is higher than 17 cm estimated by Templeman (1963) for a large net with 2.6 inch mesh codend. The selection factor,

$\frac{\text{50\% retention length (cm)}}{\text{mesh size (cm)}} = \frac{18.6}{7.2} = 2.58$, differs from the value 2.18 calculated for North Sea plaice (Beverton and Holt 1957) and for petrale sole (Ketchen and Forrester 1966). The difference is probably explained by the higher length/girth ratio for American plaice compared to the two other flatfish species.

A similar selection curve for the 1½ inch mesh net cannot be calculated, but the approximate 100% retention length, from the selection factor and length-frequency distributions, was estimated to be about 15 cm.

The plaice were measured to the nearest centimeter from the tip of the snout to the longest caudal ray (i.e. total length).

Weights were obtained from freshly caught plaice, recorded in grams after surface water had been removed with absorbent towels.

The otter trawl was towed at a constant engine revolution found to be equivalent to a speed of 2 knots over the ground. The speed was measured when possible from Decca-navigator positions and varied between 1.8 and 2.3 with a mean of 1.96 knots.

Trials indicated that the 2½ inch mesh net was most efficient in catching plaice at a speed of 2 knots. Higher and lower speeds gave lighter catches of plaice. The relatively low towing speed assured close contact with the bottom; and quantities of ophiuroids, molluscs (Yoldia sp.), and mud-dwelling holothurians (Synapta inhaerens) were caught regularly together with the plaice.

A comparison of catches from the "Whip-the-Wind" and "Sigma-t" revealed no significant difference ($0.05<p<0.10$) between the numbers caught in a series of ten parallel hauls in different parts of the Bay.

No significant difference was found between the mean number of plaice caught per minute in a series of ten hauls of 5 and 10 min duration within a small area in about 35 m depth. When necessary, adjustments were, therefore, made for differences in tow length.

Information on sampling variation was obtained by an analysis of variance of numbers in catches on three representative localities in the Bay. the "within-locality" variation served as a measure of sampling error when compared to the "among localities" variation. Data from hauls made in 1967 at the three tagging localities were used (Fig. 1; 17 hauls at A, 29 at B, and 12 at C):

Source	Sum of squares	df	Mean square
Within localities	675,717	55	12,286
Among localities	993,669	2	496,835
Total	1,669,386	57	

The low within-localities mean square shows that the sampling variation in number is small compared to the variation typically found among different sampling localities, the variance ratio being 0.025.

TAGGING

For tagging experiments, 5-15 min tows were made and the fish transferred to tanks on deck. Running sea water was supplied through hoses with intake close to the bottom. Tagged fish were measured to the nearest millimeter. The tags were yellow plastic discs, Petersen type, 18 mm in diameter, individually numbered and attached by a stainless steel pin through the dorsal muscular part of the body, above the pectoral fins. The method has been described and tested by Manzer (1952) and used on plaice by Powles (1965) and Pitt (1969). The plaice were released immediately after tagging. The tagging program was announced by posters on fish plants and wharfs in the area, and a reward was offered for the return of the tag or the tagged fish.

Tagging was carried out on three localities – A, B, and C (Fig. 1) in depths of 36, 55, and 73 m; and the number of plaice tagged were:

Locality	1966	1967	Σ
A	495	1,929	2,424
B	724	2,505	3,229
C	839	2,194	3,033
Total	2,058	6,628	8,686

RESULTS

DELINEATION OF THE STOCK

Because of the insignificant fishery for plaice the stock is virtually unexploited, and has been in this state at least since 1953 when the Bay was closed to commercial draggers. In the 2 yr previous some catches of cod and plaice were made by large-size draggers, causing the closure in order to protect the inshore cod fishery. Before these incidents, no trawl fishery was carried out in the Bay. Measurements of growth, mortality, biomass, and production, therefore, are assumed to reflect conditions in an unexploited stock.

Several independent observations suggest that St. Margaret's Bay supports a local plaice stock and that there is little intermingling between the Bay and areas offshore.

Plaice are caught off the entrance to the Bay, but in much smaller numbers than in the Bay. Catches made with the "Harengus" in winter and the "Whip-the-Wind" in summer about 10 naut mi offshore in a depth of 60 m yielded only about 1% of the number caught in comparable hauls in the Bay.

A difference in length composition between the two areas was also observed. In catches by the "Harengus" the average length of the plaice offshore was 24.4 cm compared to 28.1 cm at the same depth in the Bay. No difference in growth rates, however, was detected.

Differences in mean vertebrae number were found when comparing samples from the Bay and offshore areas.

Vertebrae numbers were determined on four samples from the Bay and two from off the entrance to the Bay (Fig. 3). All whole vertebrae between, but not including, the basioccipital and the hypural bones were counted. Pitt (1963) found no difference between the sexes, and counts for males and females were combined. Table 1 gives the results of the counting.

The vertebrae counts were compared by a series of t-tests. The obtained t-values are given on Figure 3. No significant differences were found among samples from the Bay or between samples from the offshore localities. Six out of eight t-values were significant ($p<0.05$) when samples from the two areas were compared. When the same data were treated as an analysis of variance, a similar result was found. The ratios, F, of area variance to sample variance within areas and sample variance to vertebrae variance in samples were 0.47 and 25.96 respectively. These F-values demonstrate a marked effect of area ($p<0.01$) and no effect of samples ($p>0.10$).

Pitt (1963) found only small and insignificant differences between average vertebrae numbers over large areas on the northeastern Newfoundland Shelf and the Grand Banks. In a sample from Banquereau Bank off northern Nova Scotia a mean number of 45.639±0.046 was observed.

The extent of mingling between plaice of different areas is determined more directly by the results of the tagging experiment.

Recoveries of tagged plaice were made in trawl catches by the research vessels and in gillnets by local fishermen. A very low percentage was recovered: 6.4% and 2.7% of the total number in research operations and by fishermen respectively.

Tagged plaice were recovered in all parts of the Bay, and no directed migration could be discovered. A high percentage of the recoveries was from within an area near the locality of tagging. When the Bay was divided into three geometrically equidistant areas (Fig. 1), 85% of the recoveries fell within the area of tagging. Table 2 gives the number of recoveries in a period following 6 mo after tagging up to the end of 1968.

No tagged plaice was found in the few tows made by research vessels off the entrance to the Bay, but two recaptures were made in gillnets 2 to 3 naut mi southeast of the entrance. One tagged plaice was returned from Emerald Bank (43°32'N, 62°20'W) 95 naut mi from St. Margaret's Bay, 8 mo after tagging. Except for these three, all the rest of the 232 recoveries from fishermen were from the Bay.

No data on fishing effort within and outside of the Bay are available. Gillnets are set at various localities in the Bay, but mainly along the shores in the outer part at depths around 50 m. Nets are also set off the entrance, and fisheries officers in the area estimate that the effort in a distance of 10 naut mi on both sides of the entrance is about four times the fishing effort within the Bay. The tag returns, therefore, indicate very little migration of plaice outside of the Bay.

Restricted movements of American plaice have also been reported by Pitt (1969) in Newfoundland waters. Most tagged plaice were recovered less than 30 naut mi from the tagging site even up to 7 yr after tagging. Apparently no significant migrations between coastal and offshore areas occur, and St. Mary's Bay in southern Newfoundland probably supports a resident population.

No seasonal shift in the size distribution of the plaice in the Bay was observed when analysing length-frequency data from 15 samples collected from August 1966 to July 1967. The samples, collected with 2½ inch mesh net, were from an area in the southwestern part of the Bay with depths between 65 and 80 m.

χ^2 values were calculated from a system of information statistics which is asymptotically equivalent to the χ^2 statistic (Kupperman 1959; Dickie and Paloheimo 1965). Basically, the method is a standard χ^2 test comparing the deviations of length composition of individual samples from their general mean when the samples are grouped in various ways.

The original length-frequency distributions, in 1 cm groups, were rearranged to avoid numerous small numbers. The length groups were: 15-21, 22-28, 29-35, 36-42, and 43 cm. The samples were arranged in periods of 2 mo:

	No. of samples	N
August-September	4	896
October-November	4	936
February-March	2	367
April-May	3	394
June-July	2	417
Total	15	3,510

The following approximately χ^2 values were obtained:

	χ^2	df
Within periods:		
August-September	28.8	12
October-November	30.6	12
February-March	8.2	4
April-May	41.0	8
June-July	5.4	4
Total	114.0	40
Among periods	80.2	16
Overall samples	194.2	56

$$\frac{\text{Among periods } \chi^2}{\text{Within periods } \chi^2} = \frac{80.2}{114.0} = 0.7035 \qquad p>0.10$$

The χ^2 values for each of the five periods are generally high with significant heterogenerity ($p<0.05$) in August-September, October-November, and June-July. Hence, the variance ratio, among periods/within periods, does

not reveal significant differences among the periods; and no seasonal shift in size distribution can be demonstrated.

Spawning plaice were observed in the Bay in 1966, 1967, and 1968. Plaice eggs and larvae were caught in plankton samplers in June and July in 1966. D. Sameoto (Dept. of Fisheries and Oceans, Biological Sciences Branch, Dartmouth, N.S., pers. comm.) found eggs and larvae of plaice to be common in the Bay in 1968, but caught very few eggs and no larvae off the mouth of the Bay.

Results given here lead to the conclusion that St. Margaret's Bay supports a local population of plaice and insignificant intermingling with stocks offshore take place. This result is important as estimates of, e.g., biomass and production then reflect the status of the plaice stock in the Bay and can be related to environmental conditions and measurements of production at other trophic levels in St. Margaret's Bay.

GROWTH AND MATURITY

Growth rates were determined from measurements of length and determination of age from otoliths. Otoliths were kept in a 50% aqueous solution of glycerin with a few crystals of thymol added. Hyaline rings on the unbroken otoliths were counted at low magnification with a stereoscopic microscope using reflected blue light.

On the basis of several validation techniques Powles (1965; 1966) and Pitt (1967) demonstrated that rings on plaice otoliths are true annuli, and that the hyaline rings are formed in the winter. Age readings from St. Margaret's Bay were compared to length-frequency distributions, but agreement between age determined from otoliths and length modes was only observed among the very youngest (Fig. 4). The age readings were from the samples resulting in Figure 5 and the length distribution from 22 samples collected with 1½ inch mesh net in July and August 1967 (N=6944).

Diffuse otoliths with poor readability, Class 2-type (Jensen 1965), constituted less than 5% of the samples. These otoliths gave unreliable age readings but were not excluded from the samples in order to avoid biassed growth rates. Diffuse otoliths may be associated with high growth rates as demonstrated by Powles and Kennedy (1968) for Glyptocephalus cynoglossus.

A representative picture of growth was obtained from four samples collected in 1967. The plaice were caught in a 1½ inch mesh net in the deeper part of the Bay, 40-70 m in May (N=119), June (103), July (195), and September (113). At this time of the year most of the fish have formed their annulus for the year, and the new growth is still small. The transition date, when the fish pass from one age group to the next, was set to May 1. Approximately equal numbers of otolith pairs were removed from each 5-cm length group in the samples. The average lengths-at-age are presented in Figure 5.

To obtain a mathematical expression of growth, the von Bertalanffy growth curve was fitted to the observed points following the method outlined by Ricker (1958):

$$L_t = L_\infty [1 - e^{-k(t - t_o)}]$$

L_t is the length-at-age in centimeters, L_∞ is the asymptotic length, k is the slope, and t_o is the time at which the fish would have been 0 cm if it had always grown in the manner described by the equation. The equations describing the growth are:

$$L_t = 85.5 [1 - e^{-0.04(t + 1.23)}] \quad \text{females}$$

$$L_t = 45.0 [1 - e^{-0.10(t + 0.98)}] \quad \text{males}$$

These expressions are graphed in Figure 5.

Artificially high lengths are observed among Ages 1-4. This, together with the negative t_o values calculated for the von Bertalanffy equation, are in part the result of a selection by the net for the larger plaice within each of the youngest age classes.

Plaice of both sexes grow at the same rate until Age 5. Thereafter, females grow more rapidly, reaching 30 cm by Age 9, compared to Ages 10 or 11 for males. The oldest female found was 26 yr and the longest 65 cm; the oldest male 15 yr and the longest 44 cm.

The growth patterns resemble in general those found for American plaice of other areas in the northwestern Atlantic (Yanulov 1962; Powles 1965; Pitt 1967). The rate of growth is, however, among the lower and corresponds closest to that of the northern part of the distribution area, the Labrador shelf to the northeastern Grand Bank. This should be expected because of the comparatively low, arctic-type bottom temperature of St. Margaret's Bay considering the positive association between temperature and size at comparable ages found by Pitt (1967).

No difference was observed between growth rates determined from the 1967 samples and rates computed from four samples collected in 1966. In 1966 the samples were obtained with the 2½ inch mesh net in the deeper part of the Bay in August. Figure 6 is a Walford graph with regression lines fitted to the points of each of the 2 yr. The lengths (L_t) are plotted against lengths 1 yr later (L_{t+1}). Again, the selection for large size among the younger age groups results in a bias and leads to depression of the left end of the lines. For comparative purposes, however, the Walford graph is adequate and can be concluded that the growth description (Fig. 5) is representative.

Estimates of production require data on growth, and it is important that a correct growth rate is used. Ricker (1958; 1969) points out that there are several types of growth rates. The true growth rate for estimates of production is the one that can be calculated from length (or weight) at capture and length back-calculated from otoliths or scales 1 yr previous. If size-selective mortality exists, production estimates from length-at-age data underestimate the true production.

In order to investigate the divergence between growth rates calculated from length-at-age ("X" growth rates; Ricker 1969) compared to rates from back-calculated lengths ("true" growth rates) a sample of 117 plaice from May 1970 was selected with about 30 fish chosen randomly within each 5-cm group.

A relationship between measurements on the otoliths and body length was established. Several otolith measurements were tried; and the largest radius, from the nucleus to the outer part of the hyaline rings, on the curved surface of the dorsal saccular otolith was selected as the most satisfactory.

Fish length was plotted against radius and linear regression lines calculated for males, N=81, and females, N=141, separately. No significant differences ($p>0.1$) were found between the slopes or between the intercepts on the y-axis. The material was lumped and a new equation computed:

$$Y = 5.026 + 1.436X$$

where Y is largest radius on the otolith and X is total length of the fish. This linear relationship seems adequate even if the true relationship is slightly curved (Fig. 7). The back-calculation was made only down to the length of the smallest fish at its first annulus; hence, the shape of the curve below that length is of no consequence (Tesch 1968).

The length of fish corresponding to any otolith radius was calculated from a modification of the direct proportionality formula:

$$l - c = \frac{r}{R}(L - c)$$

l = length when annulus was formed
L = length at capture
r = radius of annulus
R = total otolith radius
c = correction factor representing the body length at otolith formation.

c was found to be -3.50 (the intercept of the regression line with the absissa).

The back-calculated mean lengths at each annulus were computed from otolith measurements on paper strips obtained by means of a drawing mirror attached to the microscope.

A comparison over the whole age range of the mean back-calculated lengths with length at last annulus did not reveal any indication of "Lee's phenomenon"; i.e. older plaice showed no tendency of having a slower calculated growth than younger plaice. On the contrary, the back-calculated lengths were generally higher than the actual length at last annulus.

For production estimates a convenient measure of growth is the instantaneous rate of increase in weight. Ricker (1969) has shown that it is not necessary to compute weights in order to calculate this instantaneous growth rate, provided the exponent, b, of the length-weight relationship is

known: $w = a \cdot l^b$. (This relationship and the value of b are given on P. 17). From the above is derived the expression:

$$\log_e w_2 - \log_e w_1 = b(\log_e l_2 - \log_e l_1)$$

and the instantaneous rate of increase in weight is therefore the difference between the natural logarithms of the lengths multiplied by b.

Two sets of growth rates were calculated following the procedure above: 1) the "true" rate (Ricker 1969), based on the difference in back-calculated length between the last and the second-last annulus. This growth is that of the surviving fish of the year-class in the year prior to capture; and 2) the "X" rate (Ricker 1969), based on the mean length at last annulus for each year-class, compares sizes of surviving fish at successive ages.

The two types of growth rates are compared in Figure 8A, males and females separately. Generally, the X-type growth rates are slightly higher than the true-type, but the differences are small. In Figure 8B the true-type growth rates for females are compared to growth rates calculated from the mean length-at-age from the growth curve presented in Figure 5. These latter growth rates are of the X-type and, being based on a higher number of fish, they show less variation. Again the X-type growth rates are the higher.

These findings show that the true instantaneous growth rates found by back-calculation do not exceed the growth rates calculated from the mean individual weights at successive ages. Hence, a Lee's phenomenon is not present, or possibly the plaice present a negative Lee's phenomenon, i.e. back-calculated lengths are larger than the mean length of the year class at an earlier age. Among the very youngest age groups, however, the selective trawl sampling results in a positive Lee's phenomenon.

On the basis of this comparison of growth rates, it is assumed that estimates of the production of the catchable part of the stock from growth rates of observed lengths-at-age (Fig. 5) will not underestimate the true production.

In order to investigate if the growth was restricted to one period of the year, samples were collected with a 1½ inch mesh net in all months except January, March, and August. The seasonal growth picture is presented in Figure 9, giving data for the first five year classes. In these ages the growth is rapid and there is no sex difference.

Length measurements were also made on a sample of 41 plaice larvae caught in IKMT September 21, 1967 (D. Sameoto, pers. comm.). The mean length was 21.5 mm, and this observation is included on Figure 9. The length at hatching is 0.7 mm.

Figure 9 shows that the growth is made at a near-constant rate during the whole year but with some tendency to higher rates in May-October

compared to November-April. These results correspond to the annual temperature fluctuation near the bottom (Fig. 9; data from Platt and Irwin 1968), and to the observations of stomach content which indicate reduced feeding during early spring.

The age at which 50% of the plaice become mature was estimated from Figure 10. Following the stages in the reproductive cycle given by Powles (1965), females were classified as mature when in Stage 3, 4, 5 or 6, and males when in Stage 3 or 4. The same four samples used for the growth curves (Fig. 5) gave data for Figure 10. A curve was fitted to the calculated points. This curve was a transcript of a straight line fitted by eye to a plot of observed percentages on probit graph paper.

Half of the males are mature between Ages 5 and 6 corresponding to a length of 21 cm, half of the females between Ages 10 and 11, or 33 cm.

The observed age at maturity corresponds to the findings of Powles (1965) for plaice from the Magdalen Shallows, but differs from that of Newfoundland waters, the Grand Banks, and the Flemish Cap (Pitt 1964).

An examination of the reproductive stages in samples obtained during 1967 indicated that spawning started in the beginning of May and continued throughout June. All of the plankton samples collected in April, May, and June contained plaice eggs. Most likely the bulk of the spawning occured in May. This is in agreement with the findings of Powles (1965) and Pitt (1967).

MORTALITY

The overall proportion of female plaice in the stock was found to be 56%. Among the different size groups, however, the proportion varies greatly due to differential mortality between sexes. Figure 11 shows the percent of females within each 5-cm length group between 10 and 60 cm. Within the smaller size groups less than half were females, but the percentage increases rapidly above a length of 30 cm. These conditions are characteristic of many flatfish stocks.

Even though late maturity among females is compensated by higher longevity, the number of reproducing males present greatly exceeds that of the females.

Because of the insignificant amount of plaice fished annually in St. Margaret's Bay, fishing mortality can be disregarded and total mortality is equal to natural mortality alone.

Estimates of natural mortality were based on the age-frequency distributions of the population, i.e. catch curves. These curves, one for each sex, were determined from age-at-length data (Fig. 5) and a large representative length-frequency distribution (N=6957) based on 22 samples from randomly chosen localities deeper than 25 m. The samples were collected with a 1½ inch mesh net in 1967.

The length distribution was divided in two, one for each sex, on the basis of the smoothed sex-ratio curve (Fig. 16). The number of plaice within

each centimeter-group was distributed on the age classes in proportions determined by the age readings, and finally added up within each year class.

Catch curves for females, males, and sexes combined are presented in Figure 12.

The 100% retention length equals about 15 cm for the net used in obtaining these catch curves (see P. 3). This length corresponds approximately to Age 4 both for males and females.

The catch curves show an increasing mortality with age, lower rates up to about Age 9, and a near-constant, higher rate later.

Average mortality rates can be calculated for the fully catchable plaice by the method of Jackson (1939). This method provides a weighted estimate of annual survival rate, S:

$$S = \frac{N_2 + N_3 + \text{---} N_n}{N_1 + N_2 + \text{---} N_{n-1}}$$

where N is the estimated number at each age. For males and females combined the average annual survival rate from Age 4 to Age 22 is

$$S = \frac{4766}{5735} = 0.83$$

Annual mortality rate, A=1-S = 0.17, and the corresponding instantaneous rate of natural mortality, M, is 0.19, as obtained from the expression $S=e^{-M}$.

Similarly calculated, the annual mortality rate for females is 0.15 corresponding to M=0.16. For males the values are A=0.25 and M=0.29 from Ages 4 to 12.

The right limb of the catch curve for females can naturally be separated into two parts at Age 10. At this age 50% are mature and also there seems to be a shift in diet (see P. 20). The mortality rates calculated as above for the two periods are markedly different:

Ages 4-10:	A = 0.09	M = 0.10
Ages 11-22:	A = 0.31	M = 0.37

The catch curve of males and females combined is nearly straight from Age 9 onward, and survival can be estimated by linear regression. Equal weight is here given to all points, and this might seem reasonable with the sampling scheme used. Thus calculated, M is 0.55 corresponding to an A of 0.42. From Age 8 onward, A is 0.40. Possibly, this latter value represents the best estimate of the overall mortality in the part of the stock fully vulnerable to the 2½ inch net.

Other and independent estimates of mortality are obtained from the tagging experiments. Tagging was carried out in June, July, and August of 1966 and in June 1967, while sampling for recoveries extended through the whole period up to November 1968. With this scheme the most direct approach to an estimate of mortality is the one devised and outlined by Ricker (1958):

$$S = \frac{R_1 M_2}{M_1 R_2}$$

where S is the survival rate during the year between taggings, M_1 and M_2 the number tagged in 1966 and 1967 respectively, and R_1 and R_2 recaptures of these taggings after completed tagging in 1967.

Following this, the survival rate is:

$$S = \frac{55 \times 6628}{2058 \times 318} = 0.56$$

and the annual mortality rate, A, is 0.44. The estimate is based on all recaptures in trawl catches and gillnets during a period of 12 mo from October 1967. This allows 3 mo after the last tagging for mixing and dispersion of the tagged plaice.

It is, however, reasonable to assume that plaice tagged in 1966 were dispersed over a wider area around the tagging localities than those tagged a year later. The trawl sampling in 1968 was restricted to the vicinity of these localities, and the recaptured number of plaice tagged in 1966, R_1, is probably too low in comparison to R_2. This, and other errors as, e.g., increased shedding of the tags with time, tend to give an overestimation of mortality. This is illustrated only when recaptures in gillnets are utilized for the estimate. Here, the biassed sampling results in underestimation. The gillnets are mostly used alongshore in areas at a distance from the tagging localities, and R_1 therefore becomes comparatively too high:

$$S = \frac{41 \times 6628}{2058 \times 163} = 0.81$$

giving A = 0.19.

There is little difference between the size of tagged plaice recaptured in gillnets and in trawls. In the gillnets even small plaice are caught because the tags become entangled in the meshes. Most likely the correct value of A falls between 0.19 and 0.44 but closer to the latter, say 0.35. This rate reflects the average overall mortality of male and female plaice older than about 7-8 yr.

Large differences are found within and between the mortality estimates of the two methods, making comparisons and evaluation difficult. It seems clear, however, that the mortality increases when the plaice mature. Such an increase in mortality with age may be typical of unexploited stocks. The numerical estimates of the natural mortality reported here is presented mainly for descriptive purposes, as few estimates of this type exist for unexploited flatfish stocks. Summarized, the best estimates of the instantaneous rate, M, are:

Female age:	4-10	0.10
	11-22	0.37
Male:	4-12	0.29
Combined:	4-22	0.19
	8-22	0.37

The values obtained appear to be high for a long-lived species, but do not disagree in general with similar determinations in fished stocks. Powles (1969) determined the natural mortality of American plaice older than 8-9 yr in the southwestern Gulf of St. Lawrence. He found on the basis of age composition M = 0.26 and from tagging 0.09-0.13. Best estimates were M = 0.17, 0.13, and 0.14 for males, females, and sexes combined respectively. Ketchen and Forrester (1966) found for petrale sole that most likely a differential natural mortality was existing between sexes with M=0.20 for females and 0.45 for males. Dickie and McCracken (1955) determined the natural mortality rate in a small, discrete population of winter flounder and found M = 0.30 for both sexes combined.

Large cod is the most important predator of plaice, and small plaice were also found in stomachs of skate, sea raven, and monkfish.

Small, whitish grains, about 1 mm diameter, were noticed underneath the epidermis especially on the blind side of a high proportion of the plaice. No increase in infection rate with size was observed:

Length(cm)	<25	26 - 40	>40	
% infested	31	32	10	(N=800)

Large epithelial tumours, 5-30 mm diameter, on the skin and the fins were observed on about 0.1% of the plaice.

These skin conditions are most certainly the lymphocystis disease described on American plaice by Templeman (1965). As noted by Templeman, the plaice did not appear to be emaciated.

ABUNDANCE AND DISTRIBUTION

Preliminary investigations in 1966 showed that plaice dominated the catches generally, but very few were caught in depths less than 10 fm (18 m). To determine abundance and distribution, a sampling program was designed and carried out in August, September, and October 1966 with the 2½ inch mesh flatfish trawl. Fishing localities were chosen randomly from small rectangular areas marked on the chart and sampled as close as practically possible to this area. The duration of the tows was 8 min. One hundred samples were collected in depths below 10 fm, and the number of samples within each depth range was approximately proportional to the area of the seabed in the range. In addition, ten samples were collected in depths less than 10 fm.

The mean number of plaice per tow with 95% confidence intervals is presented in Figure 13A.

In the shallower part, less than 30 fm, catches were low and rarely more than 150 plaice were caught. In the deeper part catches were higher, usually 200-400 plaice.

The same trend, an increase in number caught with depth, was found at the tagging localities in 1966, 1967, and 1968 (Fig. 13B). There were significant differences among the years, mainly because tows in 1966 were made in all directions out from the tagging buoy, while in the later years only directions known to give good catches were selected.

The tagging experiments were started mainly to give estimates of population number in the Bay. About 1 mo after the completion of the tagging in 1966, sampling in all parts of the Bay started. No plaice, however, were recovered except on the tagging localities; and further sampling was restricted to an area within a circle of a 1 naut mi radius from the release point.

Estimates of stock numbers, therefore, are relative estimates for the three tagging localities. Calculations followed Ricker (1958). The original Schnabel method (multiple census) was used, and the 95% confidence range computed for 1/N and then inverted. The estimated stock numbers are plotted in Figure 14, together with the confidence range.

No significant difference exists between estimates from the two years. Due to the lower number of plaice tagged and recovered in 1966, the confidence ranges for estimates from this year are extremely large; and differences among the localities could not be detected. Estimates from 1967, however, show that there exist differences among the localities. The relative stock numbers are in good agreement with the abundance in different depth ranges as expressed in the catches.

An attempt was made to convert the estimates of relative abundance to estimates of numbers of plaice per hectare. Such a conversion can be made for the estimates of abundance from catches, if fishing power of the net and the area covered per tow are known.

Measurements were made on two occasions on the tracks in the bottom sediments caused by the net when towed at 2 knots. SCUBA divers found the horizontal distance between the otter boards to be 10.5 m (range 10.0-10.9) and between the wingtips of the net 4.0 m (range 3.9-4.1). The two divers observed the net in operation by hanging on to each wing. The vertical opening of the net was estimated to be 1.5 m. The net stayed close to the bottom at all times. The lower bridles, between the wingtips and the otter boards, were in contact with the bottom and a cloud of mud was stirred up. No flatfish, mainly winter flounder, were observed to escape over the headrope; and only four out of about 20 observed near the bridles escaped across these.

Observations of fish reaction to otter trawls (Blaxter and Parrish 1966; Beamish 1967) and measurements of swimming endurance (Beamish 1966) suggest that flatfish generally remain on the bottom when the trawl approaches or swim ahead of the footrope in the direction of the towing and after a short time fall back into the net. Bridles and otter boards have a strong herding effect.

Based on these observations the efficiency of the net measured perpendicular on the towing direction was assumed to be 100% for the distance between the wingtips and 80% between wingtips and otter boards. This equals a total effective width of 9.2 m. This distance was used to calculate the area swept, 100% effectively, by the net. A tow of 8 min duration at 2 knots covers 4543 m^2 or 0.45 hectare. Catches as given in Figure 13A were related to this area, and the calculated densities are presented in Table 3. The table also includes the area of the seabed within each depth range. Areas were calculated from measurements made with a planimeter on a chart.

The highest estimated density, 745 per hectare, is equivalent to about one plaice of catchable size in 13 m^2. As much as 89% of the catchable stock was estimated to be found in depths between 20 and 40 fm, or 67% between 30 and 40 fm.

Estimates of population number at the three tagging localities will be reliable if the dispersion of the tagged fish is restricted to the area sampled for tagged fish. This area was selected to be within a circle of 1 naut mi radius from the exact tagging locality. Recoveries of tagged plaice indicated that a high proportion actually remained in the area of tagging (Table 1), even after 1 yr. As the sampling was carried out within a period of 1-2 mo after completed tagging, it is probable that most of the tagged plaice were still present in the area sampled. Assuming this, the densities of catchable plaice at the three localities were:

Locality	Depth (fm)	Number/hectare	95% confidence range
1966		60	31-2377
A	20		
1967		117	86-184
1966		129	77-400
B	30		
1967		227	195-272
1966		393	241-1064
C	40		
1967		372	284-537

These densities agree rather closely with the densities calculated from fishing.

The increase in catch with depth was accompanied by a decrease in the size of the plaice. The mean length in samples from the deeper parts of the Bay was about 5 cm less than the mean lengths of plaice from shallower parts. Mean lengths of plaice caught within 5-fm depth zones are given in Figure 14. The mean lengths were calculated from 106 samples collected randomly in all parts of the Bay (see P. 14). On the figure is also included the calculated

mean lengths at the three tagging localities in 1967. The length distribution at these localities is presented in Figure 15.

Only small differences in size composition were observed among the samples from the four depth ranges below 30 fm. At shallower depths, however, more variation was found; and the highest mean length was found in samples from depths less than 15 fm.

A similar size or age segregation was noted by Powles (1969) near the Magdalen Island in the Gulf of St. Lawrence. He found that large plaice tended to remain feeding on sandy shallow banks, 10-20 fm, in May and June.

The extent of seasonal migration within the Bay and possible shifts in size distributions were not studied in detail. Samples collected in winter and the results of the tagging experiments, however, seem to indicate that the plaice migrate very little except to avoid extreme temperatures in shallow water in winter and in late summer.

BIOMASS

The length-weight relationship for plaice was established from a sample of 115 males and 220 females collected in September 1967, and from an additional sample of 277 plaice, sex not determined, caught in October of the same year. Samples were selected to give good representation in all length groups. The log-log regression of length in centimeters on weight in grams was calculated. No significant difference ($p<0.05$) was found between the slopes or intercepts of the regression lines for the two sexes, nor were any differences found between the line of the sexes combined and the line of the unsexed plaice. The data were pooled and a new equation based on all plaice calculated:

$$W = 0.005489\ L^{3.099}$$

The exponent was not significantly different from 3, and the growth can be considered isometric.

In September and October the plaice gonads are in a recovering stage and the length-weight relationship was assumed to reflect "average" condition for the year. The calculated growth in weight, when the length-weight relationship from the sexed material was used, is illustrated in Figure 16. Powles (1967) found a similar relationship, $W=0.005443\ L^{3.139}$, in a sample from the southern Gulf of St. Lawrence in October. In his sample, however, females were heavier than males at all lengths. This was, in part, assumed to be caused by sexual differences in growth and morphology.

The biomass of catchable plaice was calculated as weight in kilograms per hectare for each of the depth zones (Table 4). The biomass figures were based on the length-frequency distribution of the catches and the length-weight relationship.

There is a general increase in biomass with depth, and the overall mean biomass of catchable plaice is 39.9 kg per hectare. Because of the differences in size composition among the depth zones, the increase in biomass per hectare with depth is much smaller than the increase in number. The biomass at 25-30 fm, e.g., amounts to 50% of the highest biomass found (35-40 fm) corresponding in number to about 22%. These figures relate to only the catchable part of the stock.

The differences in contribution to the total catchable biomass within the Bay are best expressed when age compositions instead of length compositions are evaluated. The material was rearranged using the age-length keys from the 1967 material and the sex-ratio curve. The results are presented in Figure 17 as a series of histograms.

Figure 17 shows that only a few age groups are responsible for a large proportion of the total biomass. These groups, especially the 9- and 10-yr olds, are found in high numbers in only the deeper part of the Bay. Older fish found in all depth ranges contribute very little to the total catchable biomass.

It is reasonable to expect that younger plaice not vulnerable to the net may account for a substantial biomass, and an attempt was made to obtain an estimate of this biomass. Trials with a beam trawl and a lined otter trawl proved unsuccessful in catching young plaice quantitatively. Instead, the theoretical number of the young plaice present was estimated by extrapolation of a catch curve from older to younger not fully vulnerable ages.

The age distribution in the catches was calculated from a length-frequency distribution of all samples and the age-length keys. Plaice at Age 7 or 8 were found to be fully vulnerable to the net used. The average annual mortality of males and females combined for Ages 4-7 is 0.24 and for Ages 4-8, 0.20, as calculated by regression from the catch curves based on 1½ inch net. Assuming an annual mortality rate of 0.2 for Ages 1-7, estimates were made of number of plaice in each age group from Age 1 onward not vulnerable to the net.

In number, this part of the stock amounts to about 72% of the estimated total number in the stock. In biomass, however, this part is only 24%. The estimated catchable biomass in the Bay should therefore be increased by 32% to give an estimate of the entire stock, excluding the pelagic phase, Ages 0-1. When adjusted this way, the total biomass of the plaice in the Bay becomes 672,640 kg, or about 670 t in 138 km² equivalent to a biomass near 50 kg per hectare.

There are few comparable data on biomass of small unfished flatfish stocks. Dickie and McCracken (1955), however, present an estimate of the initial population of winter flounder, Pseudopleuronectes americanus, in St. Mary's Bay, Nova Scotia, before a fishery commenced. The catchable flounder biomass of this Bay, which is four to five times the size of St. Margaret's Bay, was about 3,300 t. This compares well with the plaice biomass, but differences in the general biology of the species make further comparisons difficult.

PRODUCTION AND FOOD

The observations of growth and population size have been utilized to estimate the production of the plaice stock. Because of errors likely to be inherent in the basic parameters, a simple method of calculation yielding only a gross approximation was chosen. The estimate, P, was based on increase in mean individual weight, $\bar{w}$, and number, N, present between successive ages:

$$P = \sum_{t=0}^{n} \bar{w}_t \cdot \frac{N_t + N_{t+1}}{2}$$

This is a numerical approximation to the graphic method of Allen (1951), and production is defined as by Ivlev (1945): the total elaboration of fish tissue during a specified time interval including what is formed by individuals not surviving to the end of this interval.

As the stock can be assumed to be in a steady state, the difference in number between one age group and the following, as well as the growth in weight between ages, can be used to estimate annual production. Because of the long life span of the plaice, a series of point estimates of these two parametres are available, and variations among years are dampened.

The mean individual increase in weight in each age group was computed from the growth curves in Figure 16, males and females separate (Fig. 18). The figure reflects the elaboration of somatic tissue in a year, from one summer to the next, and shows the great difference between sexes.

Mean number present in the age groups was obtained from the material used for abundance and biomass estimates. Numbers were assigned to males and females in accordance with the sex-ratio curve. This includes only the catchable part of the stock.

Production, or total annual growth of the catchable stock, was calculated for each depth zone (Table 5). The table shows a marked difference in estimated production per hectare between depths shallower and deeper than 55 m (30 fm). The increase in production with depth follows closely the increase in biomass, and production per unit area is primarily determined by the density of plaice. The difference in age composition between depth ranges has only a minor influence. The seabed area below 55 m, which accounts for 20% of the Bay, bears near 70% of the estimated plaice production. The overall annual production of the catchable stock of the Bay is about 7.6 kg per hectare.

Near the same figure was obtained when production was estimated from an Allen curve: mean individual weight plotted against number per hectare within each age group (Allen 1951). Such curves (Fig. 19) were also used to estimate the production of plaice not vulnerable to the net. As with the estimates of biomass, the average annual mortality rate for Ages 1-7 was

assumed to be 0.2. Based on this, the production of the youngest age groups not fully catchable was 2.4 kg per hectare, making the overall annual production of the Bay 10.0 kg per hectare.

The irregularity of the catch curves, especially the high number of 9-yr olds present, indicates large variations in recruitment. To correct for this variation, a smoothed curve (C; Fig. 19) was drawn by eye guided by running averages of the two catch curves and the estimated mortality of the youngest age groups. The area under the smoothed curve corresponds to a production of near 9 kg per hectare.

An estimate was made of the production of the sexual products. The weight of mature ovaries was determined on a limited number of samples. This, together with the similarity in growth pattern, indicated that it was adequate to use the relationship between ovary weight and fish length determined by Pitt (1964) for plaice from the northern slope of the Grand Banks and St. Mary's Bay. Based on this relationship, the sex-ratio curve, and the overall age-frequency distribution the production of eggs was found to be about 0.75 kg per hectare. Even though there are indications that not all females spawn every year, this figure represents a likely estimate of annual egg production. Production of sperm is lower due to the lower weight of male gonads at the same fish size. Insufficient data are available; but assuming a weight equal to half that of the ovary, and taking into account the size at maturity and sex-ratio, the calculated sperm production is 0.48 kg per hectare. The total annual production of sexual products, therefore, is probably of the order of 1.2 kg per hectare.

Comparisons between the production of the plaice, about 10 kg per hectare, and that of other marine fish stocks are difficult. Most available data refer to the yield of a fishery, usually expressed as yield per recruit rather than calculated production per unit area. However, yield figures from a well established fishery probably indicate the size of the long-term production. The plaice (Pleuronectes plattessa) fishery in the North Sea, for instance, yields about 100,000 t; and this yield has been comparatively constant over a long period. Assuming that the fishing accounts for half of the total mortality, the production is approximately 5 kg per hectare. The production of the anchovy (Engraulis ringens) off Peru, one of the most productive marine areas, is of the order of 700 kg per hectare under the same assumptions. This indicates the wide range of production of exploited marine fish stocks.

Production figures better suited for comparisons are available from freshwater fish. Allen (1951) found a very high mean annual production of 533 kg, and Horton (1961) a lower production of 100-180 kg for trout in streams, while Gerking (1962) found about 91 kg per hectare for bluegills in a small lake. These studies deal with single fish species dominating the waters, a situation similar to the plaice of St. Margaret's Bay. The production, however, is much higher. The difference is due to many circumstances of which the divergence in trophic structure may be the most important.

The production of the plaice seems to fall near the lower end of the range of productions in fish stocks - a result which might be expected considering the age composition, the feeding, and the growth of this species.

Stomachs of plaice were examined during August, September, and October with a few additional samples from winter and spring. Very few of the stomachs were empty. Food items were recorded, and the results are presented in Table 6.

Young plaice feed heavily on crustaceans, mainly mysids. Larger plaice take more ophiuroids and polychaete worms (e.g. Pectinaria hyperborea). The largest plaice feed on the same food items, but take more large bivalves (Yoldia thraciaeformis) and a large amount of sea urchins (Stronglyocentrotus sp.).

The volume of the food in the stomachs varied with season; lowest average volume was observed in December, February, and March and stayed high from May to September. A "feeding index," based on classification of the degree of fullness of the stomachs, generally followed the temperature at the bottom. A sharp increase in this index coincided with the temperature increase in early summer.

DISCUSSION

An underlaying assumption important for the interpretation and comparisons of the results is that the plaice stock is self-contained and in a steady state, i.e. constant yearly recruitment, and growth balanced by deaths.

As outlined earlier, several indices indicate that the plaice in St. Margaret's Bay pertain to a local and resident stock. However, the eggs and larvae are pelagic and confined to the upper water layer. It seems likely that a certain portion of the 0-group plaice is flushed out of the Bay and probably not counterbalanced by influx of larvae from offshore areas. The year-to-year variations in the exchange of water of the Bay is unknown, but great differences may occur resulting in variable recruitment to the stock. This, however, is but one factor which possibly leads to variable recruitment. In fact, variations in year-class strength were observed and are shown, for example, by the relatively strong 1957 year class. Such variations were also found by Powles (1969) in the Gulf of St. Lawrence. The effect of variations in recruitment on estimates of abundance, biomass, and production is difficult to assess. However, due to the high number of year classes involved the estimates may possibly represent average conditions.

The mortality rate chosen to be representative of the very young plaice not fully vulnerable to the net influence the estimates of biomass and production. Plaice aged 1 to 4 were present, but attempts to obtain quantitative catches failed. Rather than exclude these age groups, it was felt that by assigning an annual rate of 0.2 the natural situation was sufficiently approximated. With this rate the youngest age groups, excluding the first year of life, amounted to about 72% of the estimated total number and 24% the biomass and production.

As the stock was unexploited for at least 14 yr prior to the investigation and only lightly fished earlier, it is reasonable to assume that a steady state has been established, and hence the total annual population growth equals the loss to predators and natural deaths.

The relation between production and biomass is of particular interest in attempts to develop general principles that can be of use in predictions of productivity from biomass data. The ratio of production, P, to biomass, B, is:

$$\frac{P}{B} = \frac{10.0}{48.6} = 0.21$$

considering the Bay as a whole and including plaice not fully vulnerable to the trawl. Nearly the same ratio, 0.19, is found only when catchable plaice is included. The value is slightly higher, 0.23, if the rough estimate of gonad production is added.

This ratio, the turnover rate, is relatively low compared to ratios of about 0.5-0.7 found for freshwater species in lakes and streams (e.g. Gerking 1962; Mann 1965). However, a low turnover rate is to be expected due to the high longevity of the plaice, based on published information on body size in biological relationships. Dickie (1971) predicted in general the changes in turnover rate to be expected by relative changes in sizes of animals making up the biomass, and derived an indicative table of average weights and turnover rates:

$\bar{W}$, g	P/B
0.1	1.6
1	0.67
10	0.29
100	0.12
1,000	0.05

The estimated average weight of the plaice including the youngest age groups is approximately 70 g, corresponding to a predicted turnover rate of about 0.15 which falls near the observed value of 0.21.

Dickie (1971) has also drawn the attention of fisheries scientists to the comparisons of turnover rates in general terms made by Waters (1969). Waters concluded that the lifetime turnover of cohorts of animals is likely to lie close to an average value of about 4.5 within a narrow total range. With the assumption used throughout the present study that the production of all year classes in 1 yr equals the yearly production of a single year class during its entire lifetime, the production during a life span of, say, 24 yr becomes:

$$\frac{P_{lifetime}}{\bar{B}} = \frac{10 \cdot 24}{50} = 4.8$$

This is a value very close to that predicted by Waters.

In an unfished stock in steady state, the growth will be balanced by the natural mortality, M; and hence the production of the plaice stock in relation to the biomass should equal the average total instantaneous mortality rate:

$$\frac{P}{B} = M$$

For the plaice stock the equation is roughly satisfied as the P/B ratio is 0.21 and M = 0.19 for Ages 4-22, both sexes combined (see P. 14).

It is of interest to attempt to make an estimate of the food requirements of the plaice stock and compare this with data on available food. In terms of energy the total food requirements of the stock, C, should be balanced by the energy of production, P, plus the energy lost in respiration, excretion, etc., Y:

$$C = P + Y$$

For the plaice, measurements of the term Y have not been made; but the gross efficiency, P/C, of fish has been studied in general by several authors. The efficiency decreases with age, varies with the food type and ration, is influenced by water temperature and the physiological state of the fish, etc. However, as a tentative generalization a value between 5-15% seems applicable (Mann 1969), and 10% is here chosen as appropriate for a rough calculation. Following this, the required total intake of food in a year equals ten times the energy of the production. Assuming that 1 g of fish flesh is equal to 1 kcal, and 1 g of gonads is 1.7 kcal (Mann 1965), the energy equivalent of the estimated production per square meter is:

$$P = 1.00 \cdot 1 + 0.12 \cdot 1.7 = 1.20 \text{ kcal}$$

giving a food requirement of about 12 kcal per square meter per year.

Brawn et al. (1968) determined the caloric content of the benthos in St. Margaret's Bay, covering the invertebrates which generally form the diet of the plaice. They found that in depths of 28-62 m the mean caloric content of the standing crop was 76 kcal per square meter. With the short lifetime of most benthic invertebrates the production is likely to exceed the standing crop with a factor of two to three. This means that the available food energy per square meter per year is of the order of 200 kcal. In addition to this comes the energy-rich epibenthic crustaceans which are important as food for the younger plaice.

Even though the plaice might not be able to utilize all available food, it appears that the supply of suitable food is not limiting the production of the stock.

ACKNOWLEDGEMENTS

I wish to express my thanks to the members of the scientific and technical staff of the Marine Ecology Laboratory for helpful suggestions about subject matters and practical assistance during the course of the study. Special acknowledgement is due to L.M. Dickie for his direction and constructive criticism, to D.L. Peer for data on bottom configuration and sediments, and to A. MacDonald for cooperation at sea and in the laboratory.

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Table 1. Counts of vertebrae of American plaice.

Locality		Number of vertebrae				
		44	45	46	47	$\bar{V}$
St. Margaret's Bay:	1	7	31	15	2	45.22
	2	7	22	19		45.25
	3	6	44	23	4	45.32
	4	5	47	36		45.35
Offshore:	A	1	19	25		45.53
	B	2	31	34	4	45.56

Table 2. Return of tagged American plaice in relation to tagging localities. (return by fishermen, in parenthesis).

Area and year of recapture		Tagging locality					
		A		B		C	
		1966	1967	1966	1967	1966	1967
A	1967	19(7)	1	1			1
	1968	3(4)	50(31)	(5)	4(2)		(3)
B	1967			5(7)		(6)	
	1968		(3)	(5)	64(30)	(9)	(13)
C	1967			1		8	(1)
	1968				(1)	5(1)	28(6)

Table 3. Densities and stock size of catchable American plaice.

Depth range (fm)	Seabed area (hectare)	Catch (number/hectare)	Estimated stock (number)
0-5	2,229	1	2,496
5-10	1,814	4	6,665
10-15	2,126	22	46,113
15-20	1,874	62	115,719
20-25	1,582	162	256,425
25-30	1,434	226	323,434
30-35	1,329	691	919,401
35-40	1,223	745	911,520
40-45	187	541	101,239
45-50	53	538	28,511
Total	13,851		2,711,523

Table 4. Biomass of catchable American plaice.

Depth range (fm)	Biomass of catch (kg/hectare)	Estimated total biomass (kg)
0-5	- 0.4	878
5-10	1.6	2,860
10-15	9.7	20,583
15-20	22.3	41,781
20-25	35.7	56,546
25-30	56.0	80,350
30-35	103.6	137,675
35-40	112.1	137,068
40-45	97.7	18,273
45-50	93.7	4,964
Total		500,978

Table 5. Annual production of catchable American plaice.

Depth range (fm)	Production (kg/hectare)	Estimated total production (kg)
0–5	-0	
5–10	0.21	376
10–15	1.18	2,515
15–20	3.16	5,920
20–25	6.75	10,683
25–30	9.14	13,104
30–35	24.36	32,379
35–40	27.21	33,283
40–45	20.78	5,886
45–50	21.08	1,328
Total		105,474

Table 6. Stomach content. Percentage of occurence of food items.

Length (cm)	Bivalvia	Crustacea	Echinoidea	Gastropoda	Ophiuroidea	Annelida	Pisces	Others and Unidentified
<25	27	43	1	1	11	11	1	6
26-40	27	24	8	2	21	14	-	5
>40	32	7	27	1	24	8	1	1

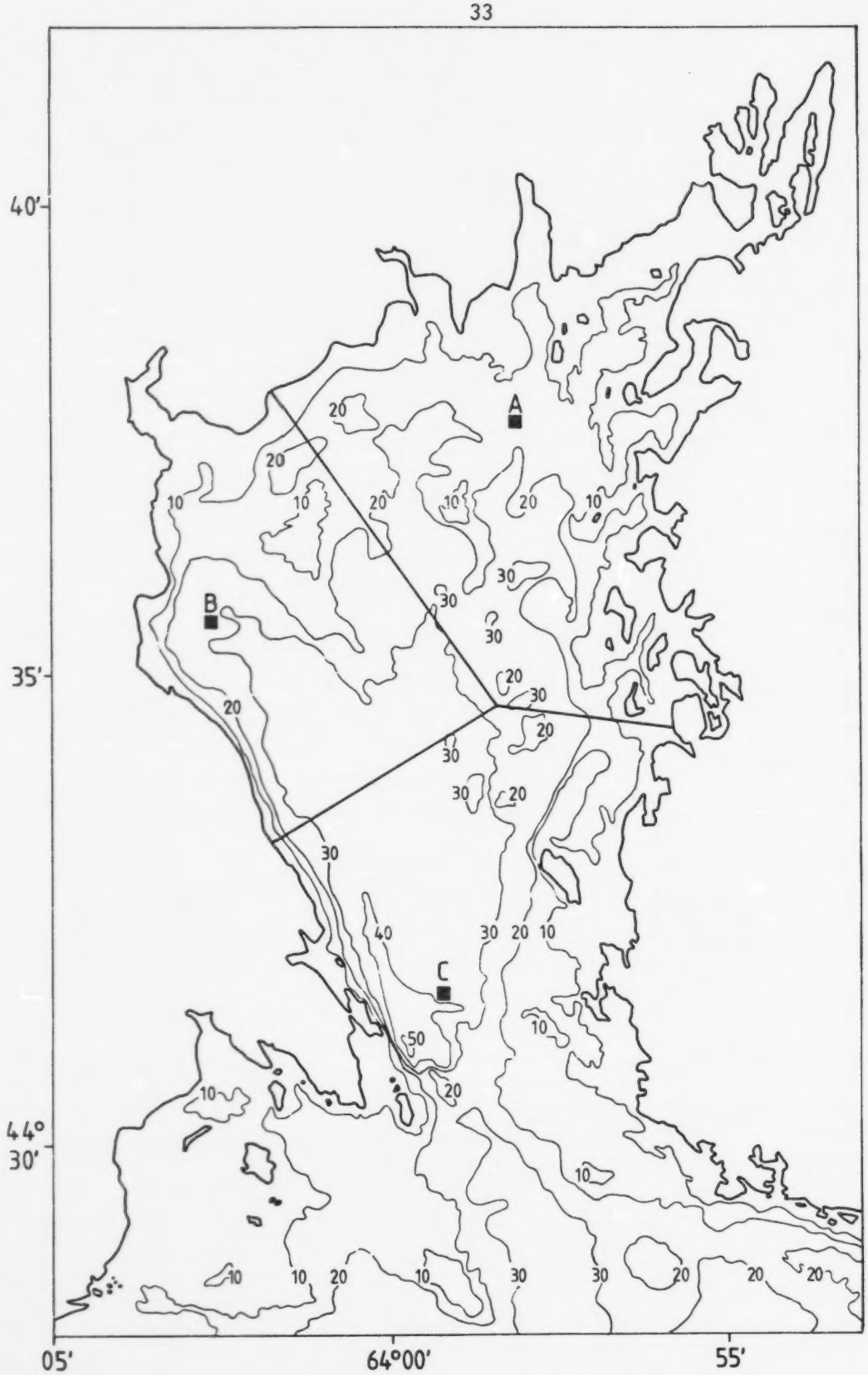

Fig. 1. St. Margaret's Bay. Depth in fathoms. Tagging localities and areas of recapture are indicated.

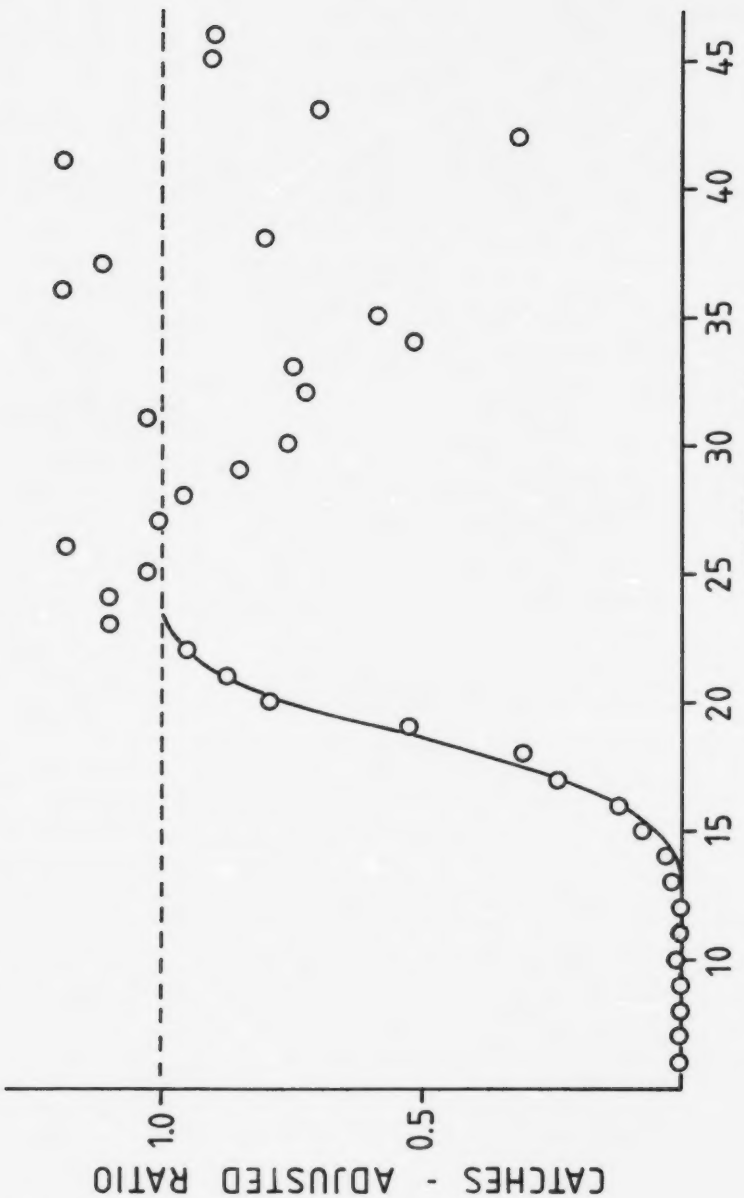

Fig. 2. Selection curve, 2½-inch mesh trawl.

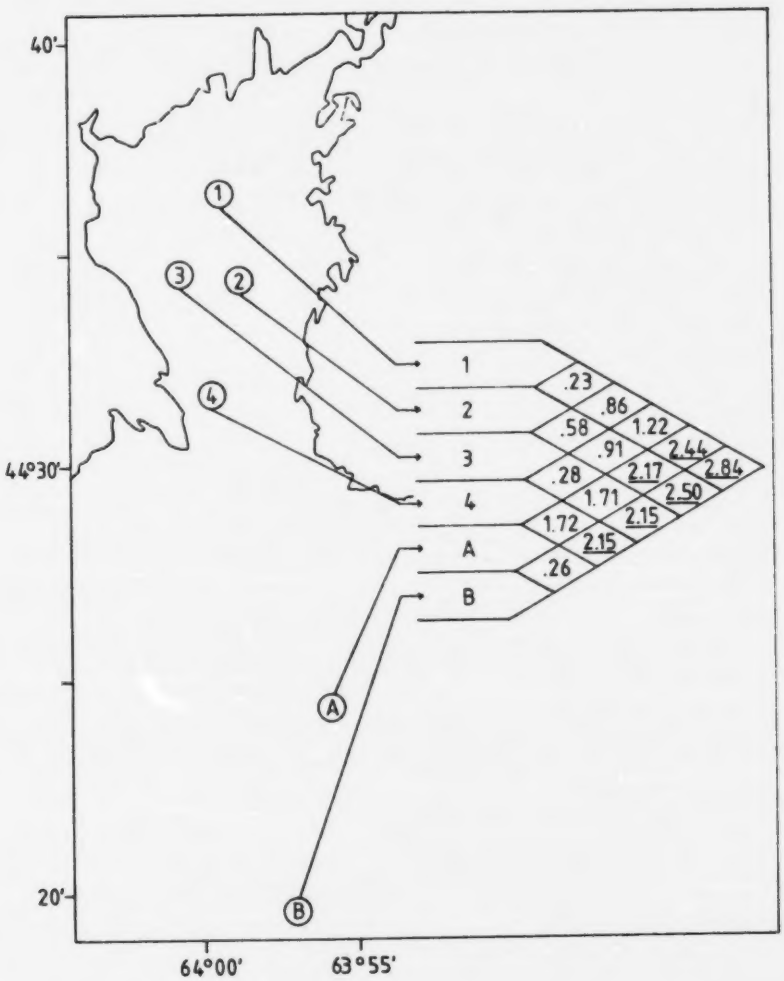

Fig. 3. Sampling localities of vertebrae counts. Diagram gives t-values obtained from comparisons between samples. Values indicating significant differences ($p<0.05$) are underlined.

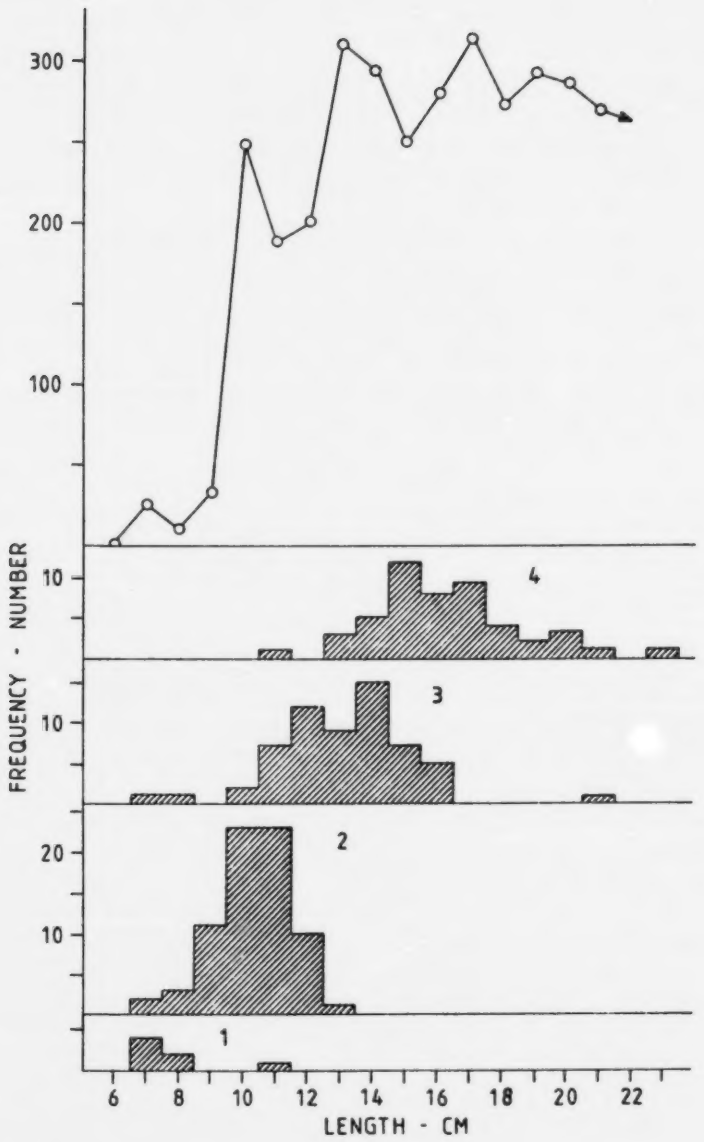

Fig. 4. Comparison between length modes and age determined from otoliths.

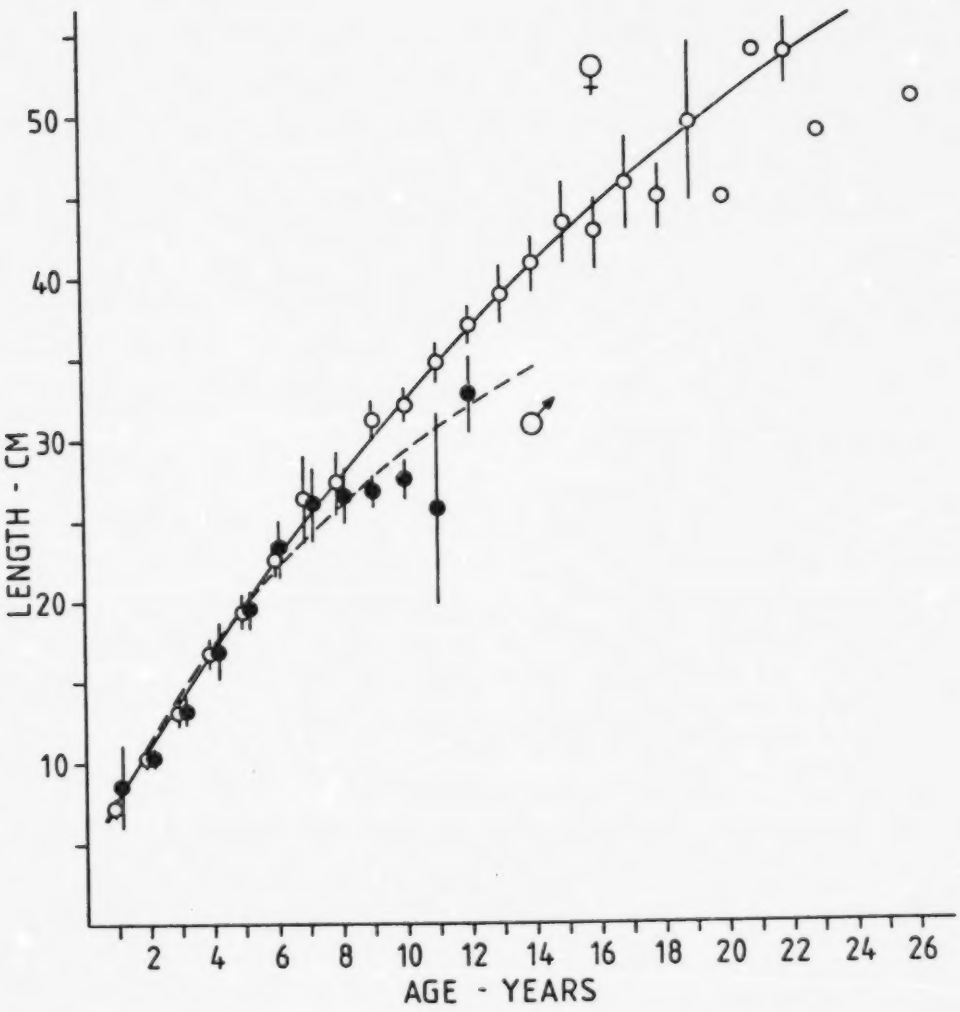

Fig. 5. Growth in length of American plaice. Bars indicate standard error of the mean. Curves are fitted according to the von Bertalanffy equation.

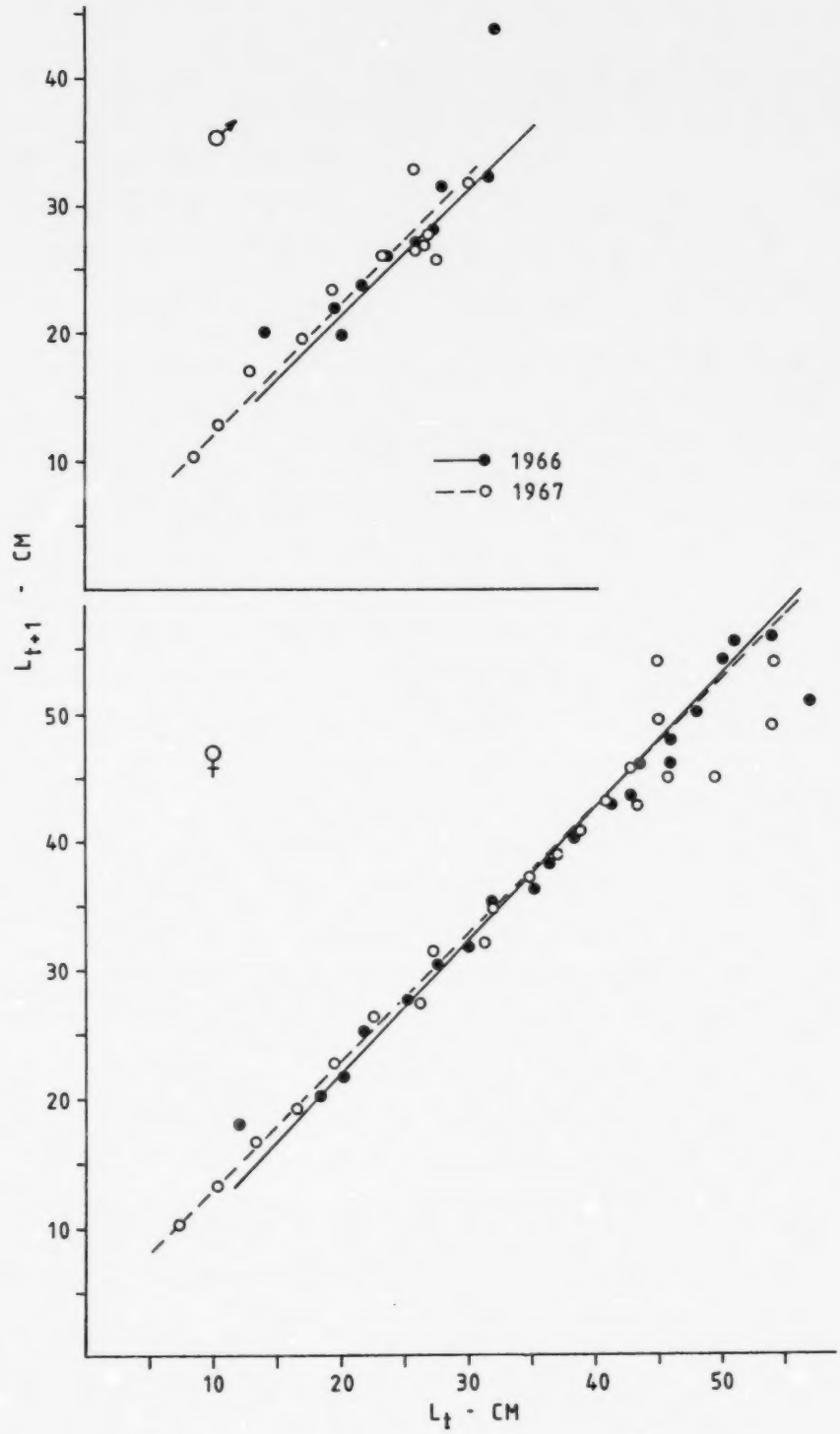

Fig. 6. Straight-line growth transformation comparing increase in length with age as observed in 1966 and 1967.

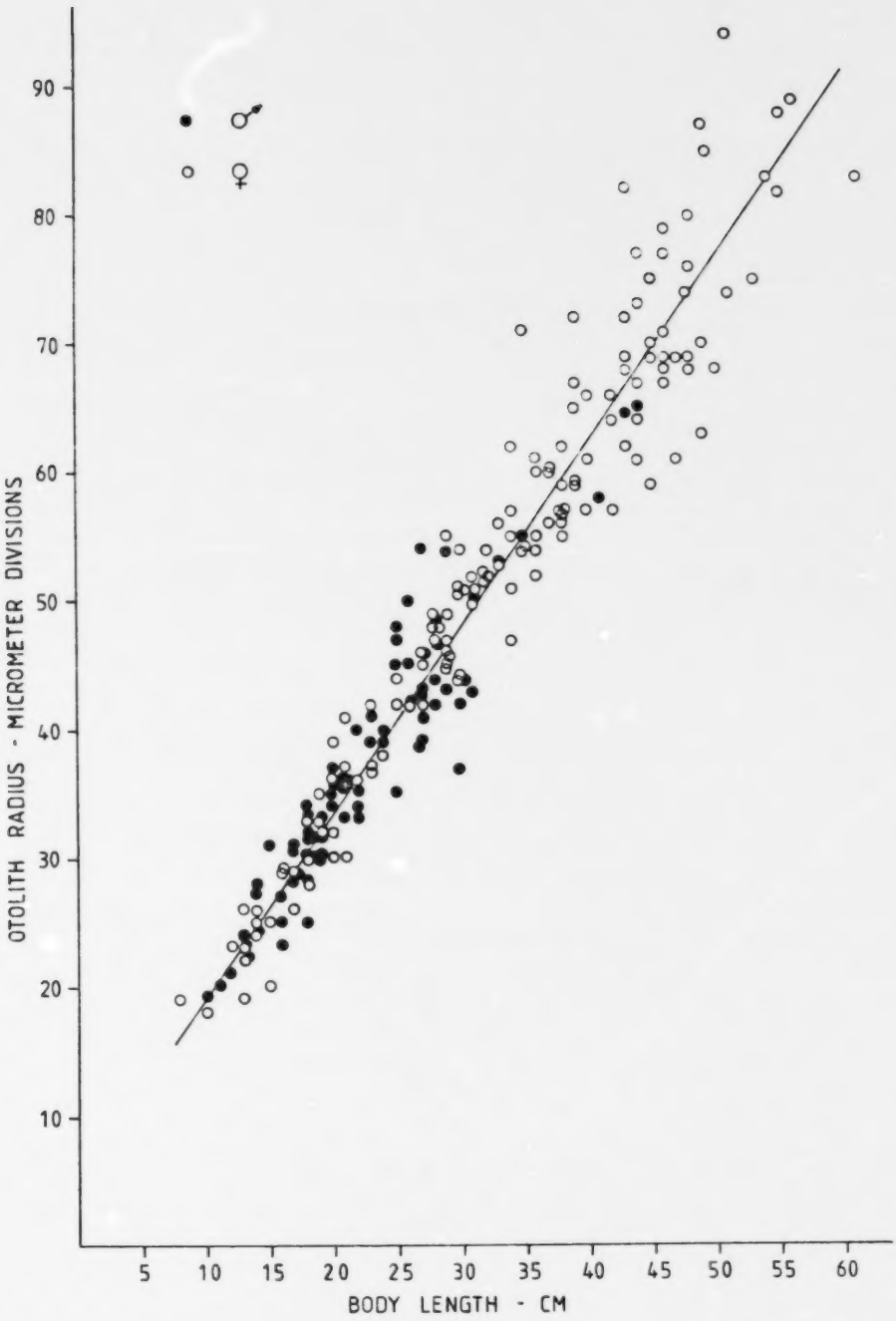

Fig. 7. Relationship between largest otolith radius and total length of fish.

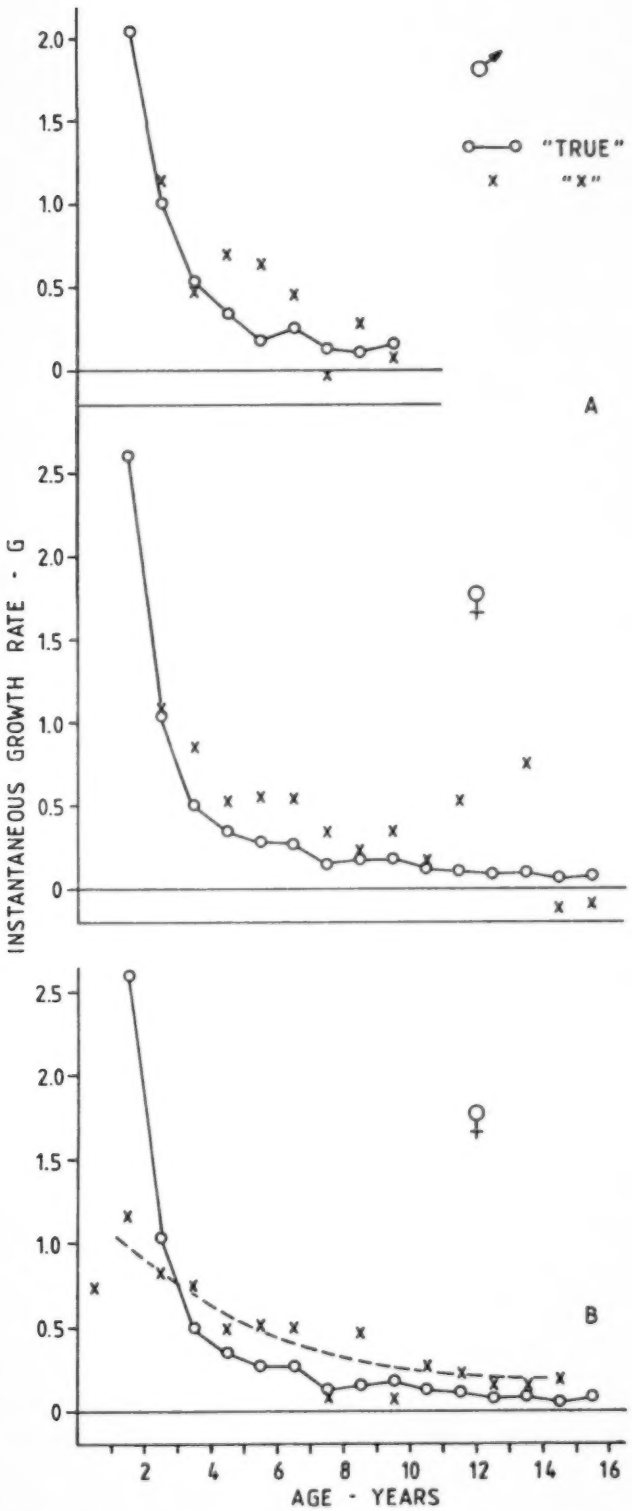

Fig. 8. Comparison between computed growth rates, "true" rates (back-calculation), and "X" rates (from length-at-age). A - from selected sample of 52 males and 65 females. B - from females of selected sample and 320 females of growth samples resulting in Fig. 5. Dashed line fitted by eye.

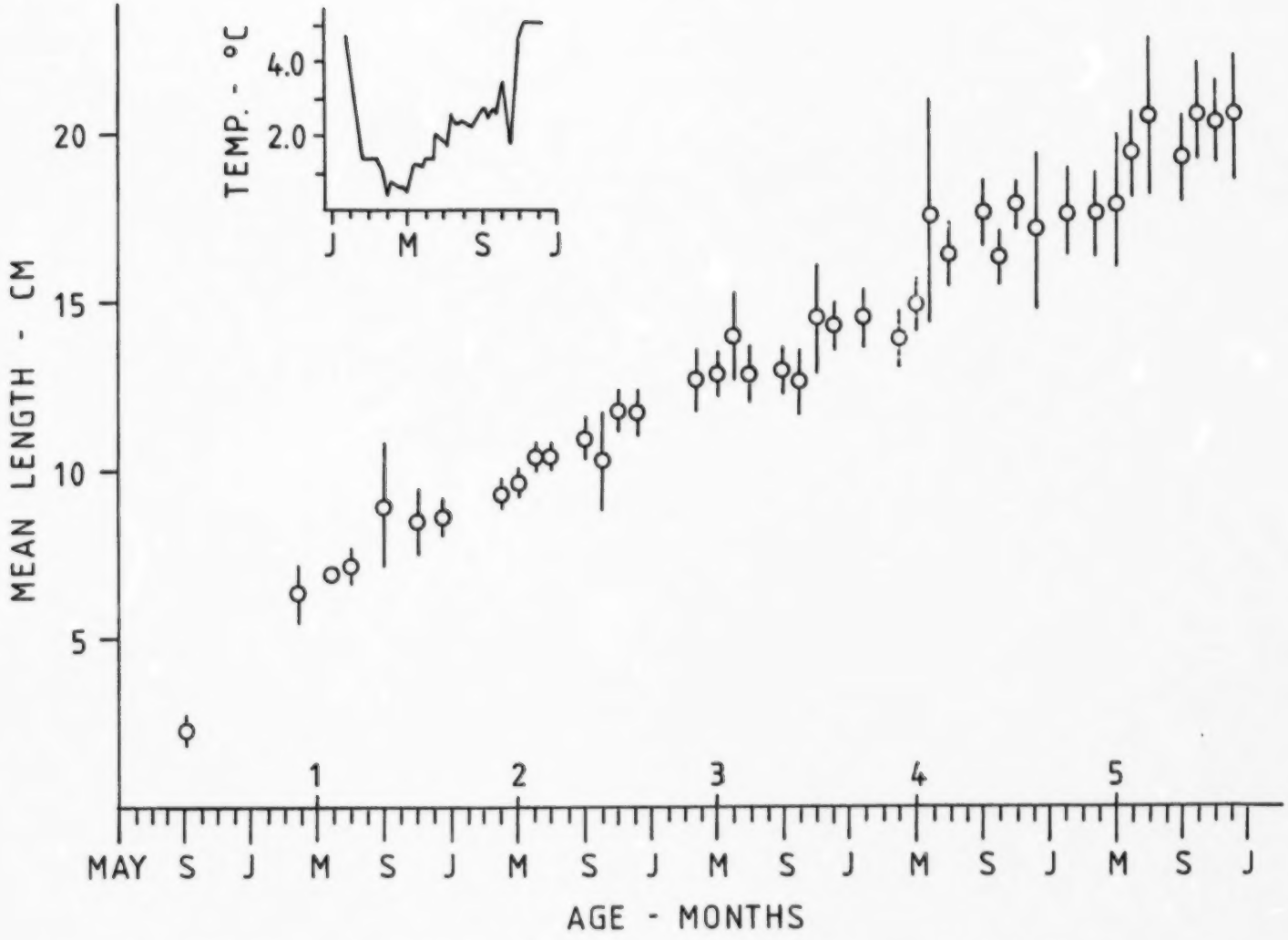

Fig. 9. Seasonal growth of young American plaice. Mean length with standard error for males and females combined. Annual variation in temperature near bottom at 53 m inserted. (Data from Platt and Irwin 1968.) Filled symbol indicates sample of pelagic larvae.

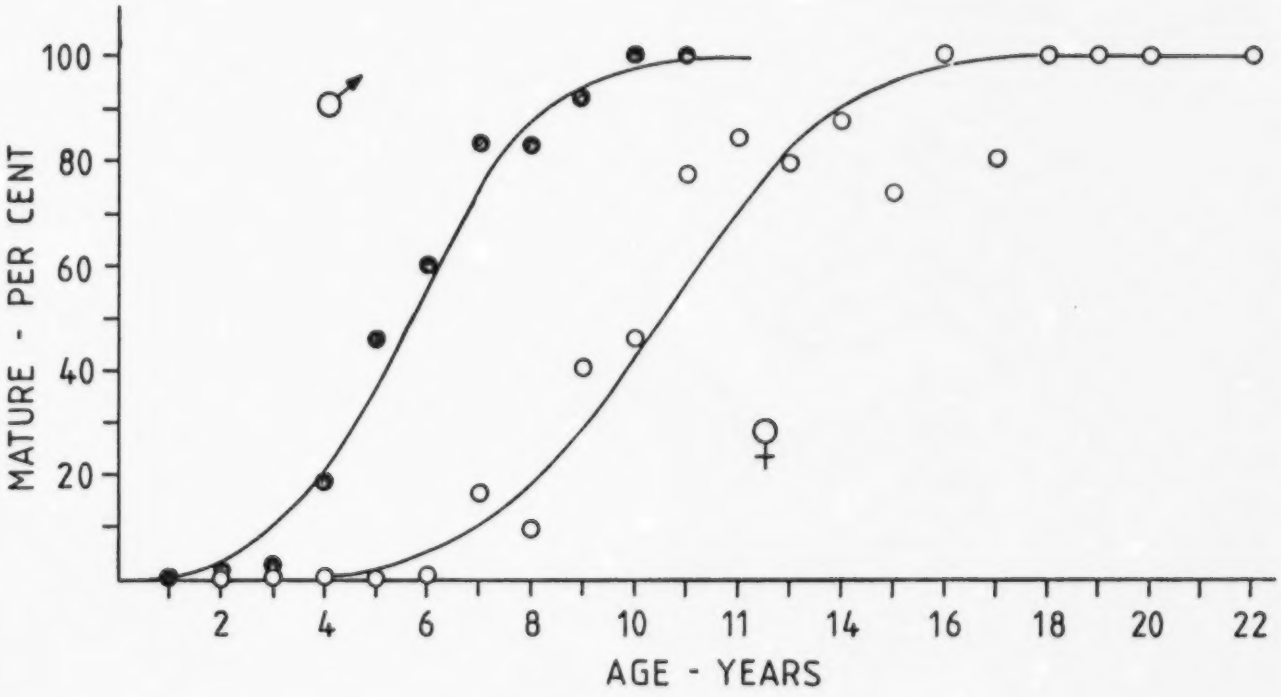

Fig. 10. Sexual maturity in relation to age.

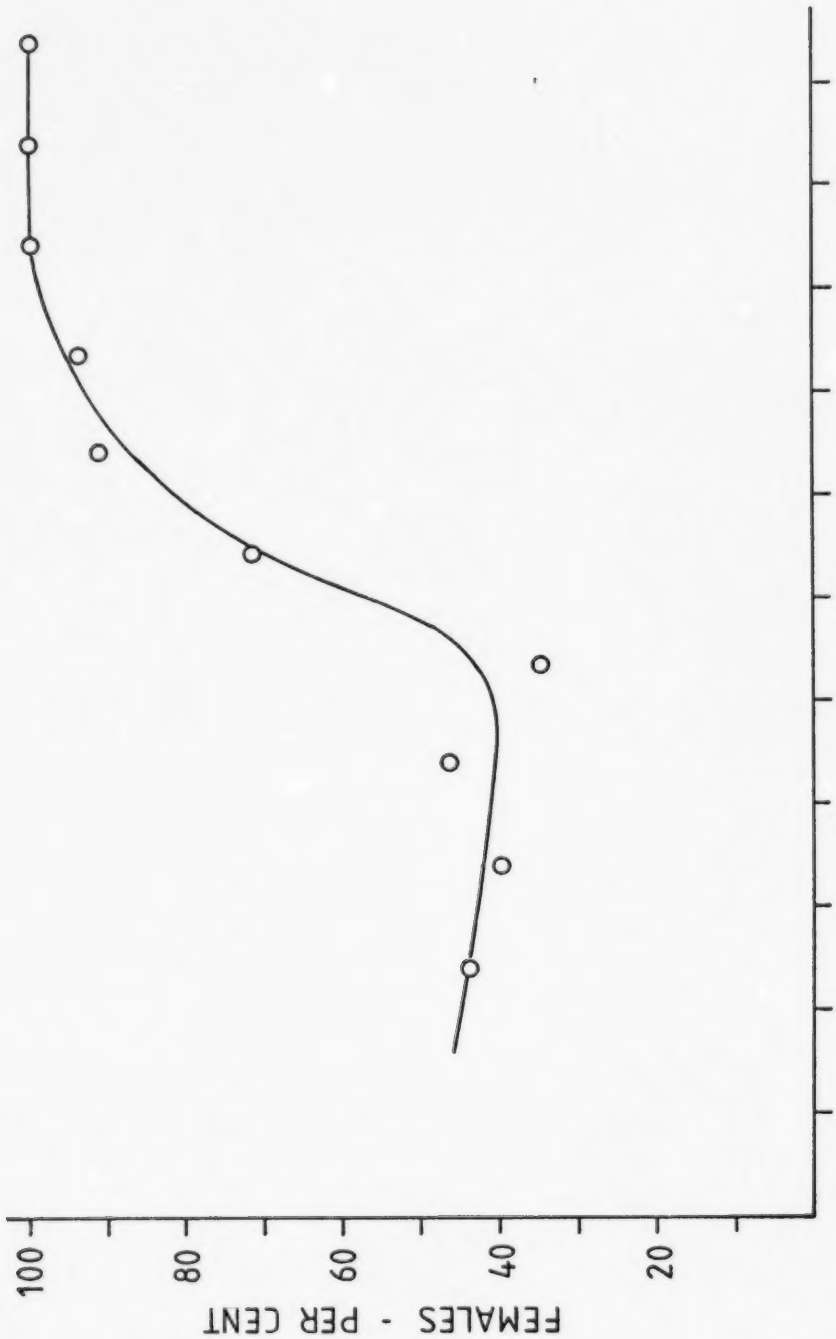

Fig. 11. Percentage of females in different size groups. Curve fitted by eye. N=2230.

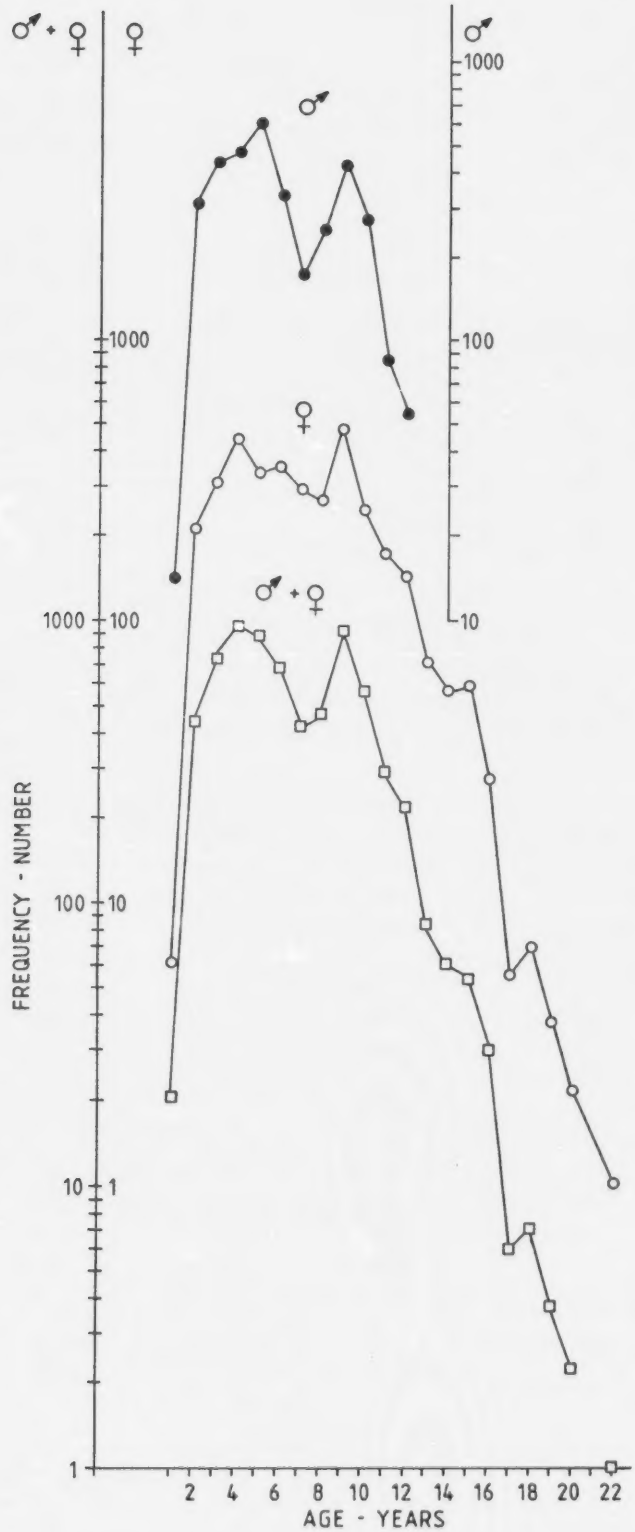

Fig. 12. Catch curves illustrating mortality rates of males (upper), females (middle), and sexes combined (lower).

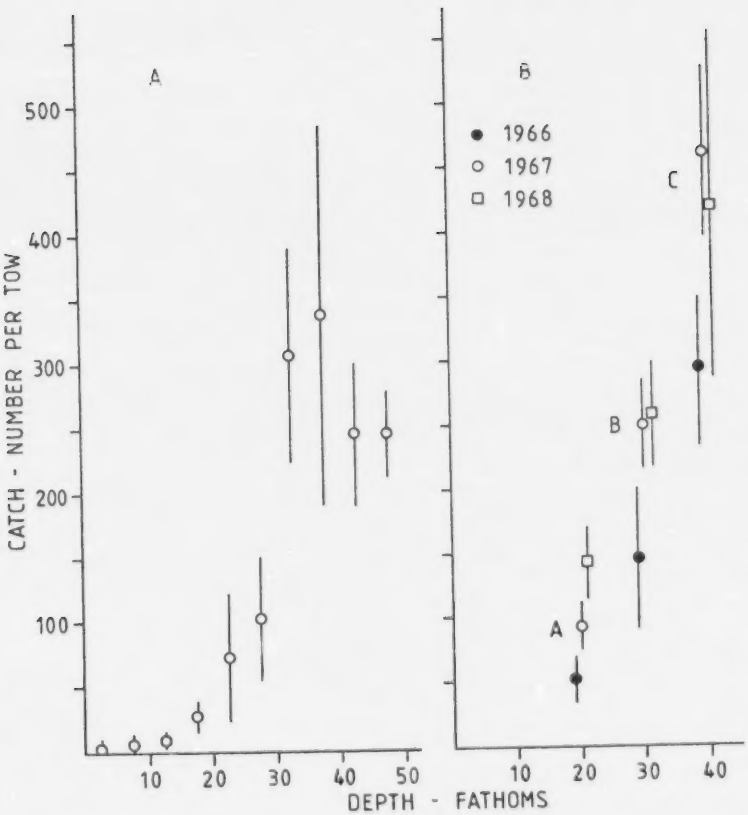

Fig. 13. Abundance of American plaice in relation to depth.
A - from randomly chosen fishing localities.
B - from tagging localities. Bars indicate standard error of mean number.

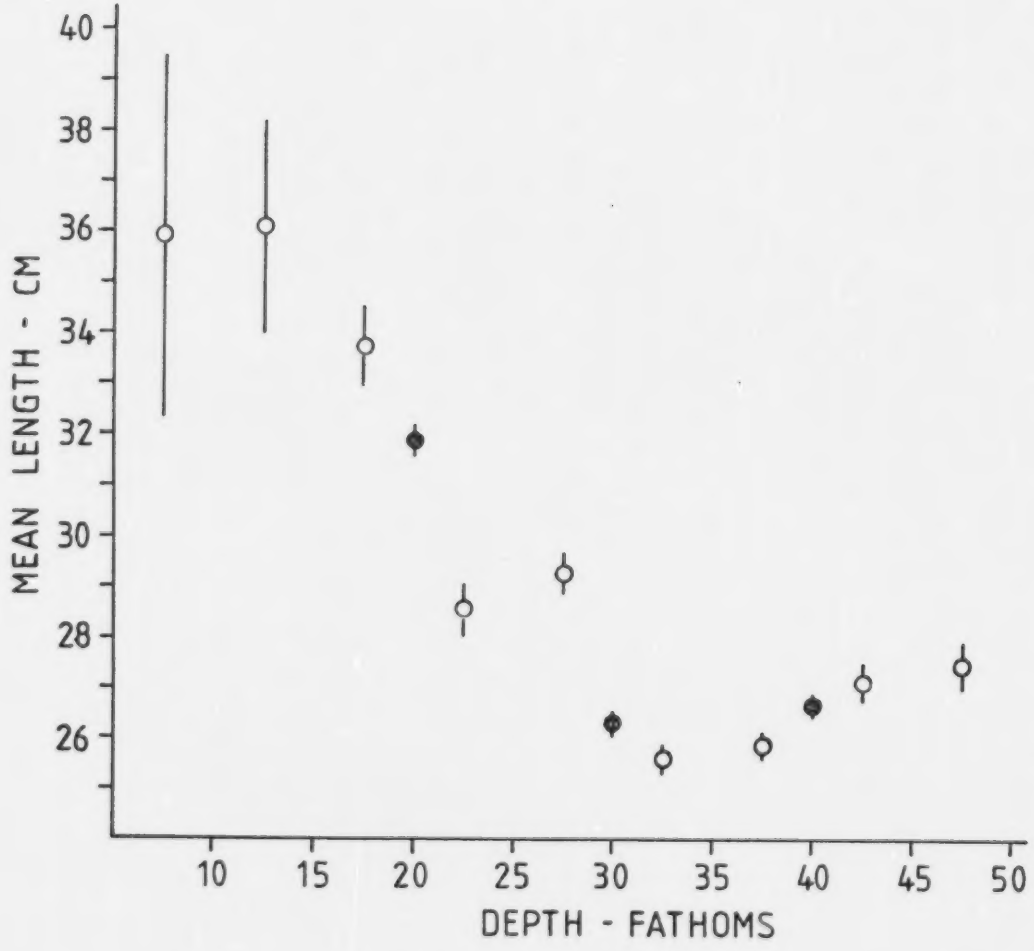

Fig. 14. Mean length of American plaice in relation to depth. Bars indicate standard error of the mean; filled symbols indicate samples from the tagging localities.

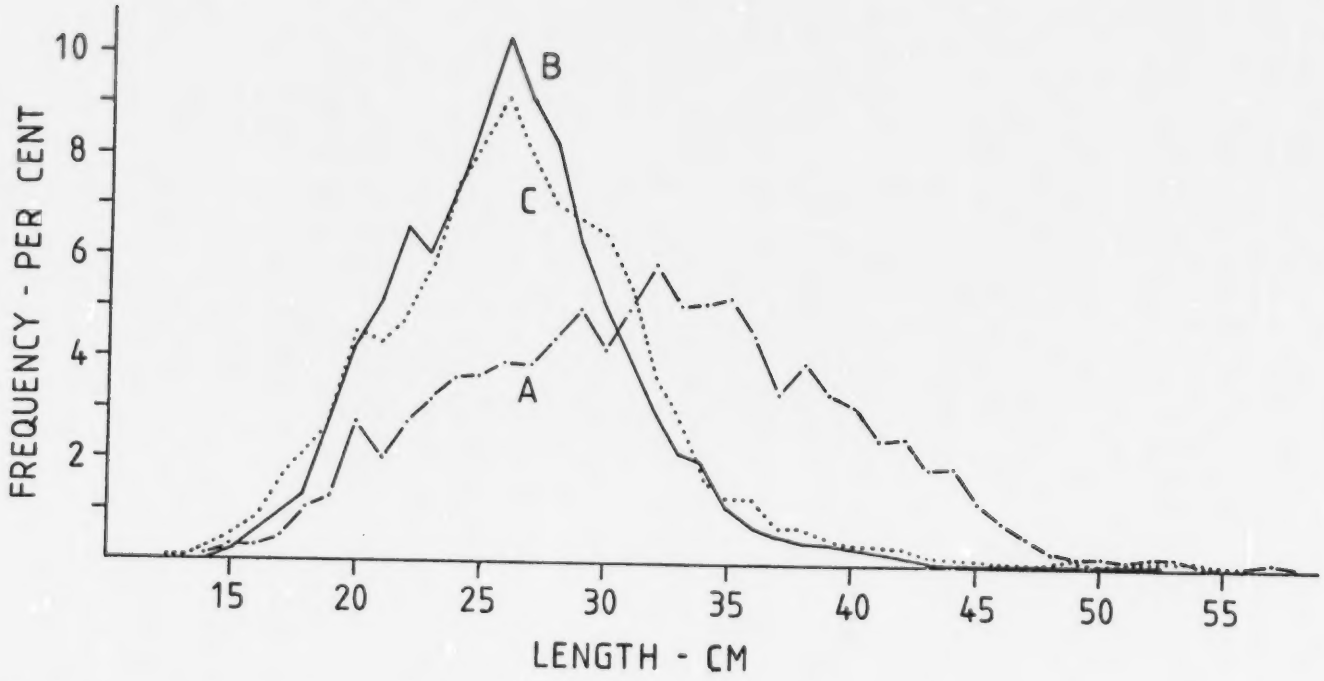

Fig. 15. Length distribution in catches at Tagging Localities A (N=2148), B (N=2892), and C (N=3107).

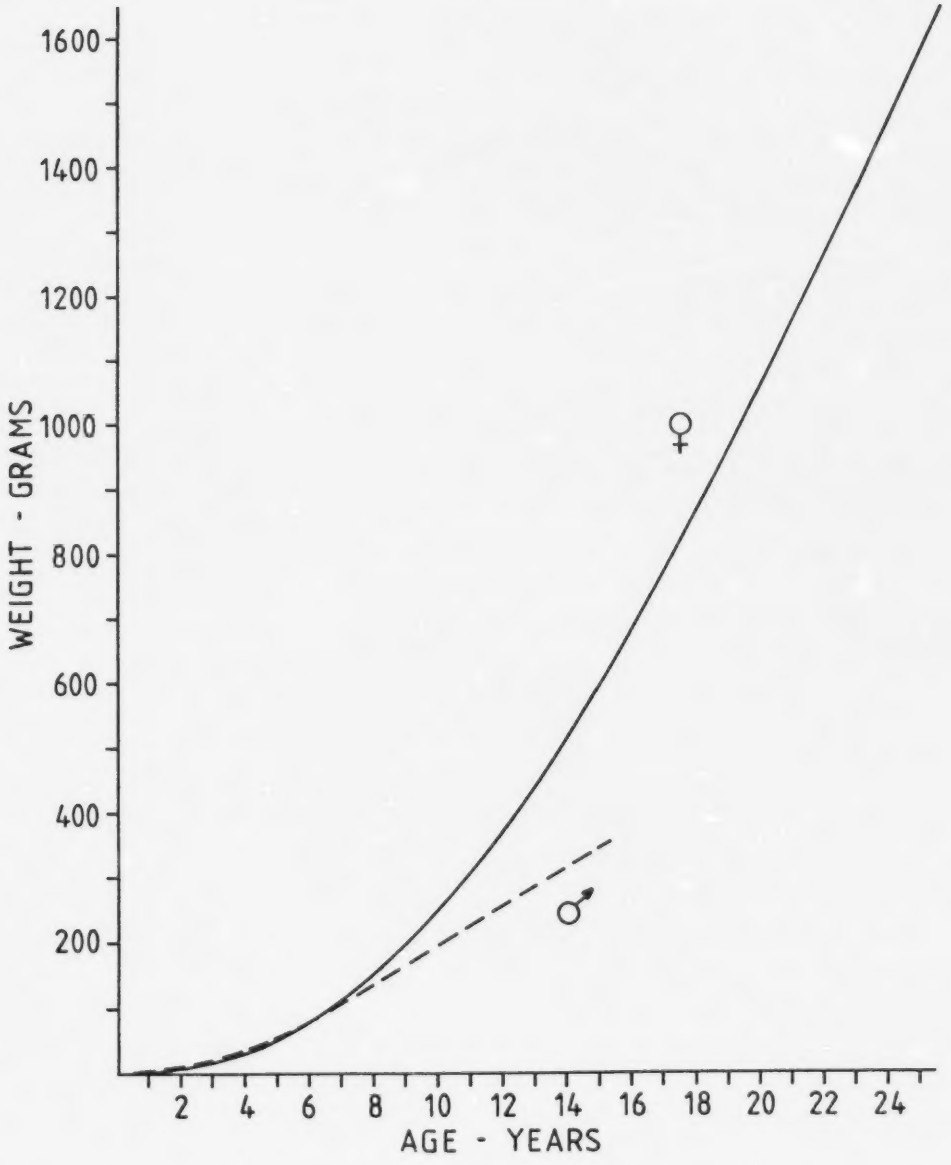

Fig. 16. Calculated growth in weight of American plaice.

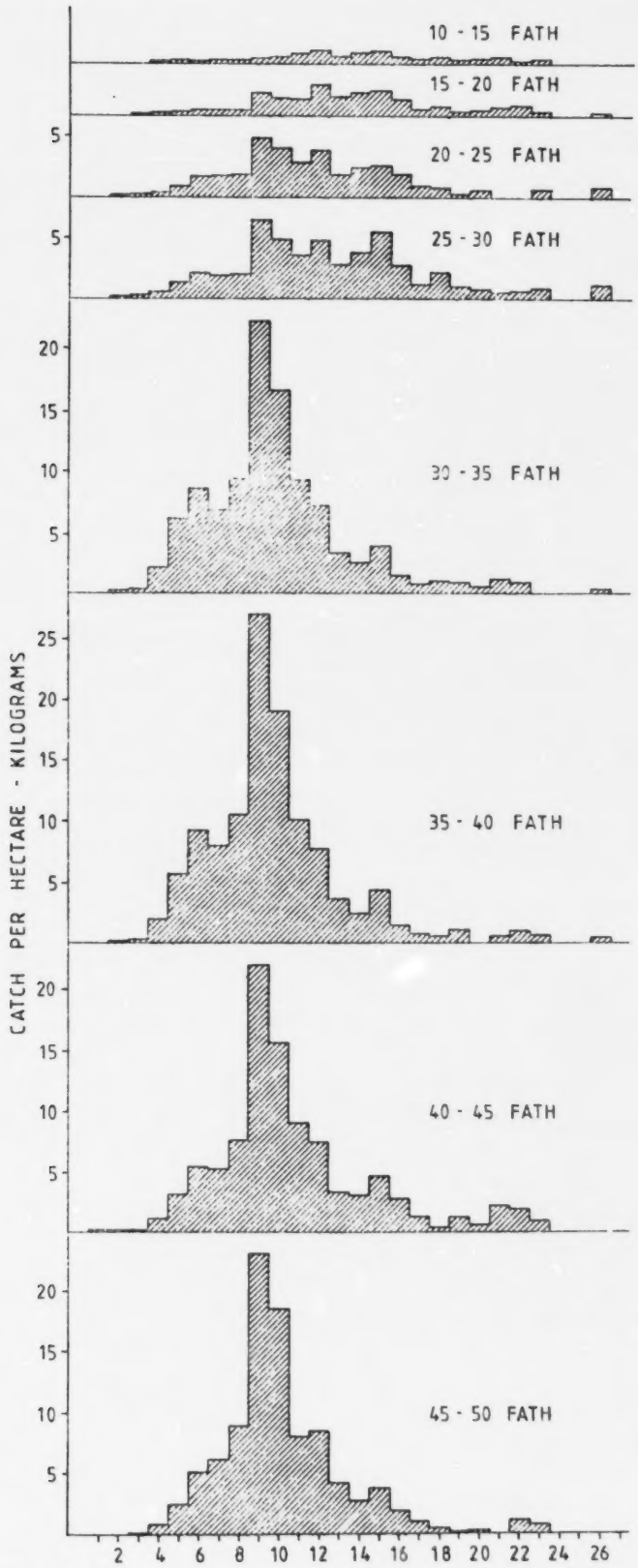
10 - 15 FATH
15 - 20 FATH
20 - 25 FATH
25 - 30 FATH
30 - 35 FATH
35 - 40 FATH
40 - 45 FATH
45 - 50 FATH
CATCH PER HECTARE - KILOGRAMS
2 4 6 8 10 12 14 16 18 20 22 24 26

Fig. 17. Biomass of catchable American plaice in relation to depth and age.

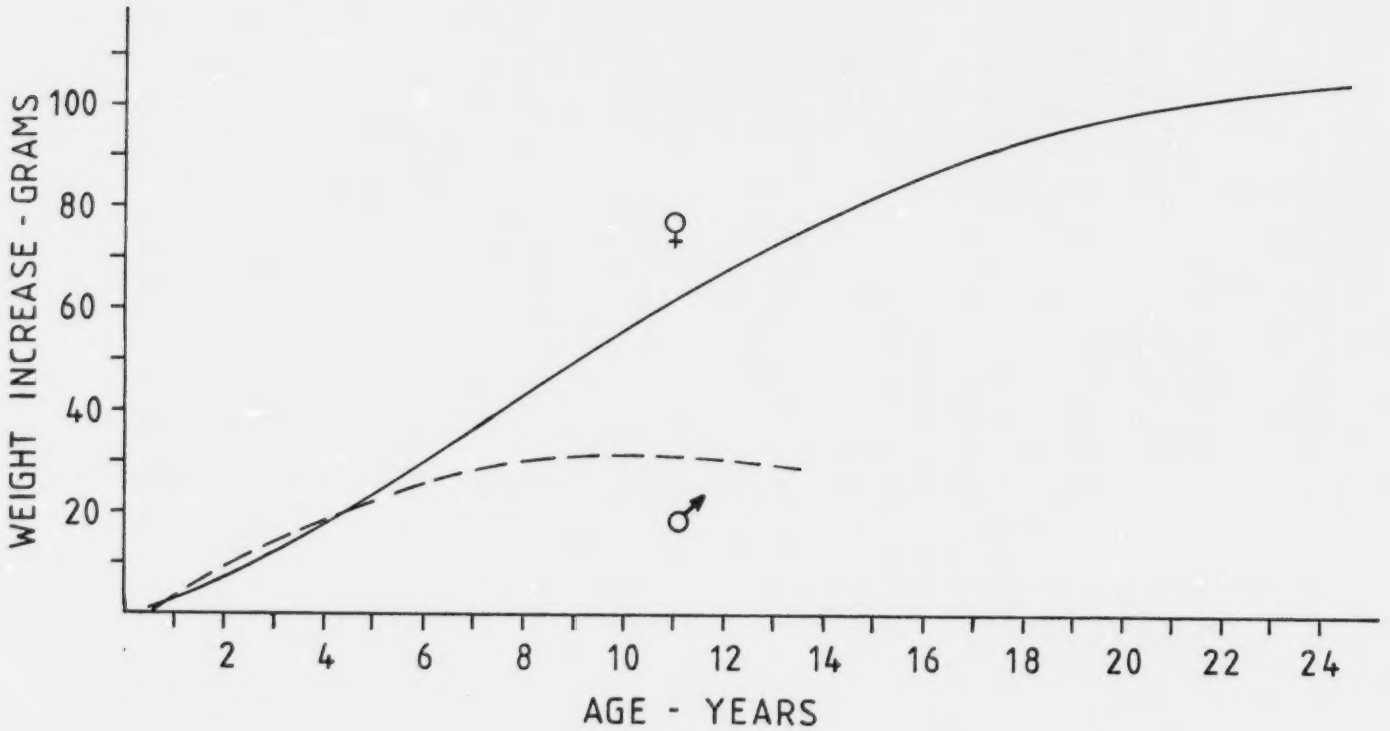

Fig. 18. Annual increase in weight within age groups of American plaice in relation to age and sex.

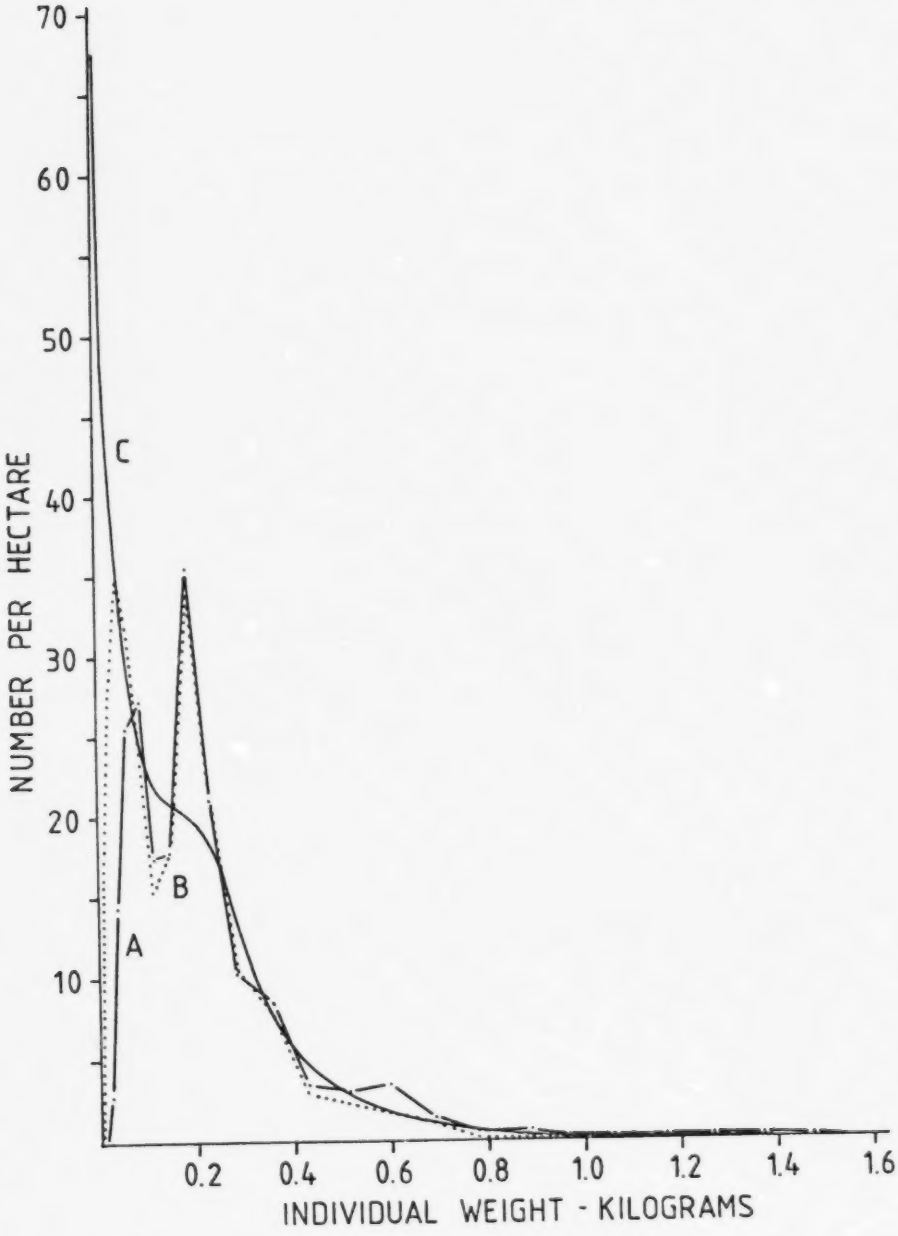

Fig. 19. Allen graph. Production is estimated by the area under the curve. Curves: A - based on average catch at randomly chosen fishing localities. B - derived from lower curve, Fig. 12, reflecting catch in small-meshed net. C - smoothed curve extrapolated to cover age groups not fully vulnerable to the nets.